ABSTRACT

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Connectivity is critical for persistence of species in the face of anthropogenic habitat destruction and fragmentation. Graph theory is a relatively new method for quantifying connectivity that has tremendous potential, but landscape graph applications to date are limited to specific conservation situations with static proportions of habitat (P). This study provides a uniform evaluation of graph metrics across wide gradients in P in both random neutral landscapes and real, forested landscapes from the Mid-Atlantic region of the United States. Such an analysis provides a background that will be valuable for future interpretation of graph metrics. Results indicate that graph metrics have characteristic forms when plotted against P that can be exploited for conservation management.

GRAPH THEORETIC CONNECTIVITY ANALYSIS OF THE MID-ATLANTIC REGION OF THE UNITED STATES

By

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Dedication

I would like to dedicate this work to several people. My wife, without her love and support I would have never made the transition from engineering to ecology, made it through this degree, or made it this far in life. My father and my grandfather: both valued education above all else, and no matter what I was involved with in my life, their first question was always "did you learn anything?" My mother, who has always supported me in just about every endeavor I've ever undertaken. My grandmother, whose prayers have kept me on the right path. And finally, I would like to dedicate this work to the oak forests and the deer, both of which seem to have a control over my life that I cannot describe, and are the basis for my passion for all things wild.

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Chapter 1: Introduction

Increases in human population and subsequent land development have resulted in substantial alteration and loss of native terrestrial habitats over much of the earth's surface. Anthropogenic habitat destruction often results in physical fragmentation of the remaining habitat, which simultaneously decreases patch size and increases distances among patches. Because fragmentation of remnant habitat can have profound impacts on a species' ability to persist on a landscape (e.g., Fahrig & Merriam 1985; Fahrig & Paloheimo 1988; Levins 1969, 1970) the combined effects of habitat loss and fragmentation are considered to be the greatest threats to worldwide biological diversity (e.g., Pimm & Askins 1995; Rapport et al. 1985; Saunders et al. 1991; Wilcove et al. 1998). Quantifying patterns of habitat fragmentation and their impact on biological systems is required if conservation biologists are to guide restoration attempts or provide suggestions for patterns of habitat loss that will reduce the effects of anthropogenic land use (e.g., Fagan et al. 2001; Moffatt 1994).

One of the first attempts to describe relationships between fragmentation and habitat loss involved use of neutral landscape models (Gardner et al. 1987). Neutral landscape models, derived from percolation theory (Stauffer 1985), were developed to assess landscape patterns that emerge as a consequence of habitat loss in the absence of ecological process (Gardner et al. 1987; O'Neill et al. 1992). Neutral landscape analysis showed that the severity of habitat fragmentation is a function of the proportion (or percent) of the landscape occupied by the habitat type of interest

(P). As P falls below a critical value (P_C) the probability that a percolating cluster will form changes from 1.0 to 0.0 (Gustafson & Parker 1992). A percolating cluster (also referred to as a spanning cluster) is a large habitat patch (or cluster of connected patches) that touches two opposing sides of a square map. Thus, spanning ability has parallels with the movement, flow or rate of spread characteristic of a wide array of biological processes (With 1997). As P falls below the critical amount, the spanning cluster fragments into multiple, smaller patches. A small change in P near the critical value results in a rapid, nonlinear reduction in the size of the largest patch, a loss of spanning ability and an increase in the number of patches; hence P_C is referred to as a critical threshold (With et al. 1997).

Various researchers have hypothesized that the shift in pattern when the proportion of habitat falls below P_C should have parallels in real landscapes (e.g., Gardner et al. 1987; Gardner & O'Neill 1990; Gustafson & Parker 1992; Johnson et al. 1992; O'Neill et al. 1988; Tischendorf 2001), resulting in dramatic changes in population dynamics as fragmentation accelerates below the critical threshold. Studies of real landscapes (Gardner et al. 1987; Gardner & O'Neill 1990; Gustafson & Parker 1992; Johnson et al. 1992; O'Neill et al. 1988; Tischendorf 2001) have revealed critical thresholds similar to those predicted by neutral landscape analysis, prompting assessments of forest fragmentation based on these thresholds (e.g., Gardner et al. 1992; Riitters et al. 2000; Riitters et al. 2002; Wade et al. 2003). Habitat in real landscapes tends to be more aggregated than random (Gardner et al. 1987) and cannot be ranked automatically as being fragmented or not based on P alone. There is a greater probability, however, that habitat in real landscapes will lose spanning ability

and become fragmented at habitat proportions smaller than the critical threshold (Gardner & O'Neill 1990). Ranking of geographic regions based on fragmentation risk at the continental (Riitters et al. 2002) and global (Riitters et al. 2000; Wade et al. 2003) scale, using P_C values derived from neutral models, allows conservation biologists to focus on those geographic regions with the highest risk of habitat fragmentation (With 1997).

Habitat fragmentation has differential effects based on species gap crossing ability, and the study of connectivity assesses the functional relationships among patches in a fragmented landscape (With et al. 1997). The coupling of neutral landscape models with metapopulation theory has allowed researchers to assess population dynamics of real or hypothetical organisms in simulated fragmented landscapes (With 1997). Many of the results predict critical thresholds in P below which fragmentation compounds the negative effect of habitat loss. Lande (1987) developed a general metapopulation model applied to neutral landscapes and predicted an "extinction threshold" for $0.25 < P < 0.5$. Bascompte & Sole (1996) and With & King (1999b) advocated species-specific extinction thresholds might be useful for conservation management. Sole et al. (2004) predicted through simulation in neutral landscapes that biodiversity collapse is a threshold phenomenon related to critical habitat proportions. Additional theoretical work (e.g., Fahrig 1998; Gamarra 2005; With & King 1999a) has shown that the increase in distances among patches observed when $P < 0.2$ is responsible for rapid population declines and extinction. Collingham & Huntley (2000) predicted reduced migration rates of woody plant species across neutral landscapes when $0.1 < P < 0.25$ due to increased distances among patches.

Other simulations of organism movement (e.g., Flather & Bevers 2002; King & With 2002; Tischendorf 2001; With 1999; With et al. 1997) have shown thresholds in population response in the range $0.3 < P < 0.5$. The variation in predicted P thresholds in the aforementioned simulations is due to differences in the models and the inherent ability of species to cross gaps that form among patches. Despite the differences in the population and neutral landscape models used, simulations consistently predict threshold responses primarily accounted for by the proportion of habitat and structural changes that occur below critical thresholds in P.

There is a building body of literature that suggests that some real-world populations exhibit threshold responses across critical thresholds in P that are similar to those predicted from neutral landscape models. Andrén (1994) analyzed the literature on bird and mammal species in archipelago ecosystems and found that such thresholds may exist for $0.1 < P < 0.3$. With & Crist (1995) showed that experimental insect assemblages had population distributions predicted by hierarchical neutral map simulations. Aphid populations in experimental agricultural landscapes exhibited thresholds in population distributions for $P < 0.2$ (With et al. 2002). Forested landscapes in Australia were observed to have a sharp decline in woodland-dependent bird species richness for $P < 0.1$ (Radford et al. 2005). Other observations of bird species in forested settings showed transitions in probability of persistence for 4 of the 15 examined species to be in the approximate range $0.02 < P < 0.5$ (Villard et al. 1999). Bascompte & Rodriguez (2001) found woody plant species richness decreased rapidly for landscapes with $P < 0.35$, suggesting that species richness is a threshold phenomena related to critical values of P.

Based on the empirical work cited above, critical thresholds predicted from neutral landscapes can be useful for conservation management of real landscapes (e.g., Moffatt 1994; Riitters et al. 2000; Tischendorf 2001; With & King 1999b), although this view is not universally accepted (e.g., Monkkonen & Reunanen 1999). Habitat loss is a primary threat to biodiversity: focus on thresholds instead of habitat loss may result in undesirable conservation outcomes (Fahrig 1999, 2003). Populations generally decline with decreasing habitat amount, and the use of thresholds may be misconstrued to imply that populations will persist until 50% to 90% of habitat is lost (Monkkonen & Reunanen 1999). Such assumptions may lead policy makers and land managers to adopt overly simplistic decisions that could lead to adverse conservation outcomes (Lindenmayer & Luck 2005). Muradian (2001) suggested that threshold phenomena related strictly to P are not applicable to broad classes of organisms or to diverse geographic regions; threshold behavior, if predicted by more complex (and realistic) metapopulation models, should be used instead.

Conservation management often involves broad geographical regions with large numbers of patches, making parameter-intensive spatially explicit population models cumbersome (Calabrese & Fagan 2004; Urban 2005). The commonly used alternative, traditional landscape structure metrics (e.g., Hargis et al. 1998; McGarigal et al. 2002; Neel et al. 2004) are easily calculated with landscape information alone, yet their interpretation requires experience (e.g., Corry & Nassauer 2005; Trani & Giles 1999) and avoidance of pitfalls (Li & Wu 2004). In addition, traditional landscape metrics have limited ability to incorporate species-specific traits such as gap crossing ability, which limits their utility in assessing how organisms utilize

resources in fragmented landscapes. Exceptions are simple indices based on proximity or nearest neighbor distance, but it is questionable if these approaches are useful for inferring connectivity in fragmented landscapes (Bender et al. 2003; Moilanen & Nieminen 2002; Winfree et al. 2005).

Graph theory provides a cost-effective method for analysis of connectivity among patches in fragmented landscapes (Calabrese & Fagan 2004). Using graph theory one can assess connectivity at multiple scales through specification of species-specific gap crossing ability in the calculation of graph metrics (Bunn et al. 2000; Keitt et al. 1997; Rothley & Rae 2005; Urban & Keitt 2001; Urban 2005). Depending on habitat configuration, there may be multiple isolated networks. In general, a graph with one large network of patches is considered more connected than a graph with multiple, isolated networks of patches.

The benefit of graph-based approaches is that they can rapidly provide insights into potential connectivity with a paucity of data, they do not require excessive computational resources, and landscape graphs can be used as a framework upon which to build more complex spatially explicit population models (e.g., Bunn et al. 2000; Keitt et al. 1997; Rothley & Rae 2005; Urban & Keitt 2001; Urban 2005). The fundamental basis for the analysis is the landscape graph, the attributes of which change in response to habitat amount, habitat arrangement and species gap crossing ability (Acosta et al. 2003; Bunn et al. 2000; Cantwell & Forman 1993; Keitt et al. 1997; Ricotta et al. 2000; Urban & Keitt 2001). Landscape graphs are in essence meta-models (Urban 2005), that incorporate features of spatially explicit population

models and can be used to rapidly analyze very large extents (Calabrese & Fagan 2004).

The main objective of this thesis is to examine the behavior of landscape graph metrics as a function of the proportion of habitat, P. Because all of the landscape ecological applications of graph theory to date have quantified graph metrics for specific conservation scenarios, a uniform evaluation of graph metrics across broad gradients in P has not been performed. Fragmentation occurs to varying degrees as a function of P and across critical thresholds, therefore landscape graph metrics may have scale dependent characteristic responses to this process, the nature of which will be useful for future ecological applications of graph theory and landscape analysis in general.

Chapter 2: Methods

2.1 Landscape Selection

2.1.1 Random Landscapes

Binary random neutral 128 x 128 pixel landscapes were generated using the program RULE (Gardner 1999). Although these pixels are dimensionless, I assigned a 30m pixel resolution to be consistent with the forested landscapes analyzed. Contiguous habitat patches were defined using the 8-neighbor rule. Ten replicates each were generated at habitat proportions of 0.05 to 0.4 in increments of P = 0.05. Replicates were not generated for P > 0.4 because $P_C \approx 0.4$ for the 8-neighbor rule (Plotnick & Gardner 1993). These random landscapes are essentially not fragmented for higher P values.

2.1.2 Real Landscapes- Study Area and Sampling Scheme

The study area is defined by the United States Geological Survey (USGS) National Land Cover Data (NLCD) mapping zone 60, 2001 (http://seamless.usgs.gov, downloaded October, 2004). The data set has a 30m resolution. The extent of zone 60 is 111,408 km^2 and includes the entire Chesapeake Bay and whole or portions of several states in the Mid-Atlantic region including Delaware, Maryland, New Jersey, Pennsylvania, Virginia, and the District of Columbia (Fig. 1). Of the 111,408 km^2 contained in this region, 90,467 km^2 are land and 20,941 km^2 are water. Forest was chosen as the focal habitat because it represents the primary potential natural vegetation for the Mid-Atlantic region (Kuchler 1964; Whittaker 1975; Wickham et al. 1999). Zone 60 was chosen because it encompasses wide gradients in human land

use patterns and forest fragmentation (Weber 2004; Wickham et al. 1999; Widman 1999).

The Level II modified Anderson scheme (http://www.epa.gov/mlrc.html) was reclassified to a binary landscape using ArcView GIS 3.2, such that types 41 (deciduous), 42 (evergreen) and 43 (mixed) were reclassified to forest or "habitat" and the remainder of land cover types were classified as non-forested matrix. Contiguous forest habitat patches were defined using the 8-neighbor rule.

Three hundred ninety-five non-overlapping 512 x 512 pixel sample landscapes were extracted from region 60 (Fig. 2) using an ArcINFO Arc Macro Language (AML) script. Extracted landscapes that included only water were excluded from analysis and were not included in the count of 395 samples. The sample landscapes represent a total of 93,192 km^2 of the original 111,408 km^2 extent.

2.2 Traditional Metrics used in the Analysis

I calculated the proportion of habitat (P), the largest patch index (LPI) and the number of patches (NP) for each sample (real) landscape using the FRAGSTATS software package (McGarigal et al. 2002). The largest patch index represents the dominance of the largest contiguous patch on a landscape (McGarigal et al. 2002). It is calculated as the area of the largest patch divided by the total area in the extent such that for any habitat amount $0.0 < LPI < P$. A version of LPI representing the proportion of habitat contained in the largest patch was calculated as

$$A'_{LP} = \frac{LPI}{P}$$

$$0.0 < A'_{LP} \leq 1.0$$

The subscript LP refers to the largest contiguous patch on the landscape. A'_{LP} is undefined when P = 0.0 and equals 1.0 when the total amount of habitat is contained in one large patch. Both NP and A'_{LP} characterize the structural fragmentation of a landscape.

2.3 Graph Metrics

The graph metrics analyzed represent attributes of landscape graphs that are formed by considering all patches within a specified threshold distance (d_t) of each other to be connected. A threshold distance is considered to be the maximum distance across non-habitat an organism is expected to move (i.e. gap crossing ability). In graph terminology, patches that are connected are considered "adjacent", a network of adjacent patches is called a "component" (isolated patches are also called components), and the number of patches in a component is referred to as the "order" of that component. The "largest" component in a landscape is that with the largest order. In this study I used the closest edge Euclidean adjacency rule (D'Eon et al. 2002; Dale et al. 1994; Keitt et al. 1997; Rudd et al. 2002). I calculated four commonly used graph based metrics (Urban & Keitt 2001): the order of the largest component (O), the graph diameter (d(G)), the number of components (NC) and the number of edges (NE). The graph diameter is the "longest shortest path" across the largest component. It was calculated using Dijkstra's algorithm (Dijkstra 1959) as the longest distance across matrix elements an organism would traverse to span the largest component, with the stipulation that the stepping stone traversal within the component comprised optimized, shortest path routing (Urban & Keitt 2001). The

number of edges is the total number of connections among all habitat patches in a landscape.

For the purpose of efficiently comparing results from multiple landscapes across a wide range of habitat amount, O and NC were normalized to a common scale (0.0 to 1.0). Metric normalization was accomplished by modifying the original FORTRAN77 source code (Urban & Keitt 2001), which was provided by Dean Urban, Duke University, in January 2005.

The normalized order of the largest ordered component (O') was calculated as

$$O' = \frac{O}{NP}$$

$$\frac{1}{NP} \leq O' \leq 1.0$$

The normalized order of the largest component describes the dominance of the largest component relative to the total number of patches on a landscape. For a given landscape, as threshold distance increases O approaches NP and O' approaches 1.0. Because O' is based only on the proportion of patches included in the largest component, it does not provide information on the amount of area contained in the largest component. The normalized area of the largest component is calculated as,

$$A' = \frac{A_{LC}}{A_{tot}}$$

$$0.0 < A' \leq 1.0$$

where A_{LC} is the aggregate area of all patches in largest component and A_{tot} equals the total amount of habitat in the landscape. The normalized area of the largest component is undefined for landscapes with no habitat ($A_{tot} = 0.0$), and approaches

1.0 as the amount of area in the largest component approaches the total amount of area on the landscape.

A second area-based metric (η) was calculated to represent the proportion of habitat area in the largest component relative to the proportion found in the largest patch.

$$\eta = \frac{A'}{A'_{LP}}$$

I developed this metric (η) to understand how much habitat area is to be gained by virtue of connectivity for a specified threshold distance. If $\eta < 1.0$, the largest component contains less area than the largest contiguous patch. If $\eta = 2.0$, the largest component contains an aggregate area twice that of the largest patch. In the limiting case where no connections exist among patches on a landscape, every patch on the landscape is a component with order 1 and the definition of the largest ordered component is arbitrary. In this case I set A' = A'_{LP} and $\eta = 1.0$.

This ratio allowed me to ask how often the aggregate area of the largest component is smaller than that of the largest contiguous patch (i.e. $\eta < 1.0$)? If $\eta < 1.0$, the largest component cannot contain the largest contiguous patch. It is often assumed that habitat clusters form as constellations of smaller patches in close proximity to a large source patch (the largest patch on the landscape), and by determining how often $\eta <$ 1.0, I calculated how many landscapes from the sample set violated this assumption for different threshold distances.

The metrics O', A', η and d(G) were calculated for the largest ordered component in each sample landscape for each threshold distance. The following metrics were calculated on all landscapes with more than one patch as measures of overall

landscape connectivity and include contributions from all habitat patches on a landscape.

The normalized number of components (NC') was calculated as

$$NC' = 1 - \frac{NC}{NP}$$

$$0.0 \leq NC' < 1.0$$

If no connections exist among patches for a given threshold distance, NC equals NP and NC' equals 0.0. Small values of NC' indicate low connectivity and values of NC' approaching one indicate that the patches are coalescing into a small number of connected components.

The gamma index (γ), commonly used in transportation network analysis, has been offered as a measure of landscape connectivity (Acosta et al. 2003; Forman 1995; Ricotta et al. 2000). The gamma index quantifies the connectivity of the landscape graph as

$$\gamma = \frac{NE}{3(NP - 2)}$$

where 3(NP – 2) is the number of edges of the corresponding planar graph where NP > 1. A planar graph is a complete graph with the maximum possible number of non-redundant pair-wise connections assuming that no edge intersections are formed (Ricotta et al. 2000). If $\gamma = 1.0$, there are as many connections in the sample landscape as in the fully connected corresponding planar graph. If $\gamma < 1.0$, the landscape may be fully connected, with every habitat patch connected by at least 1 edge to a single large component. However, if many patches are connected to the

component by one edge only, the component is at higher risk of disruption from removal of habitat patches. If multiple edges exist among patches, removal of single patches due to habitat loss will have less of an effect on overall connectivity. When $\gamma > 1.0$ patches are connected to one another via multiple edges, implying a lower sensitivity of landscape graph to connectivity disruptions caused by patch removal. For comparison, the maximum number of edges that can form among patches in a landscape is 0.5 NP(NP-1).

2.4 Parameterization

2.4.1 Threshold Distances for Random Neutral Landscapes

Contiguous habitat patches were defined by the 8-neighbor rule. Graph algorithms were used to analyze the formation of components for threshold distances of 60m and 90m. Threshold distances were measured pixel-centroid to pixel-centroid (e.g., McGarigal et al. 2002), so at 30m pixel resolution 60m and 90m threshold distances are equivalent to 1 and 2-pixel gap crossing abilities respectively. It can be shown that a 1 and 2-pixel gap crossing ability using Euclidean nearest neighbor adjacency is the equivalent of using the 12 and 24-neighbor rules for cluster definition. The largest component formed by the graph algorithm using a 60m threshold distance is equivalent to the "largest patch" defined by RULE (Gardner 1999) using a 12-neighbor rule. Similarly the largest cluster formed using a 90m threshold distance is equivalent to the largest patch using the 24-neighbor rule. These threshold distances were chosen for the purpose of visualizing the trends in graph metrics rather than to associate them with the behavior of the metrics calculated for real landscapes. The

random landscape size of 128 x 128 pixels was chosen because it was of sufficient size to model 1 and 2 pixel gap crossing abilities without suffering from the influence of boundary effects.

2.4.2 Threshold Distances for Real Landscapes

I calculated the graph theoretic metrics outlined above for threshold distances of 120, 180, 360, 450, 990 and 1,500 meters. These distances span a range of the gap crossing or dispersal abilities of many vertebrates and plants native to the Mid-Atlantic region (Tables 1 & 2). Woody plant species have seed dispersal distances that can be considered equivalent to gap crossing ability (Table 2) when non-habitat matrix elements are considered unfavorable for establishment. Many non-forested areas in the Mid-Atlantic region are often unfavorable for establishment as these areas are maintained in permanently developed states (e.g., agriculture, developed, urbanized areas and impervious surfaces) and represent gaps that must be crossed if species are to colonize forest patches where they are not currently established (Dunn 1991). All of the woody plants considered, with the exception of *Carya* spp. and *Quercus* spp., have wind blown seed dispersal mechanisms. Although hickories and oaks have large seeds that typically establish near the maternal plant, the larger gap crossing ability for these genera is due to vertebrate assisted dispersal. Gray squirrels and Blue Jays are known to cache nuts of hickories and oaks up to 1.5 km from forest edges (He & Mladenoff 1999; Sork 1983).

2.5 Relationships between graph metrics and habitat proportion

2.5.1 Random Neutral Landscapes

The metrics O', A' and d(G) were plotted against P for threshold distances of 1 and 2-pixels to explore the behavior of the largest component as a function of habitat proportion. The metric NC' was not calculated for these random map simulations because for the chosen gap crossing abilities (1 and 2-pixels) the behavior of NC' is the equivalent of the number of patches as reported by programs such as RULE (Gardner 1999).

2.5.2 Real Landscapes

A cumulative frequency distribution for P was constructed by sorting and ranking landscapes in ascending order of P, and plotting the ranking versus P. Curves of both NP and LPI versus P were generated from the series of 395 sample landscapes. For all sample landscapes and all six threshold distances outlined in the previous section, curves of O', A', η, d(G), NC' and γ versus P were generated. LOWESS regression was used to generate trend lines for the curves of O', A', η, d(G) and NC' versus P. LOWESS regression is a non-parametric form of weighted moving average (Kutner et al. 2004). In this work, LOWESS regression was parameterized with a tri-cube weighting function, a locally linear approximation and a sliding window that used 25% of the data for regression calculations at each data point.

Chapter 3: Results

3.1 Neutral Random Map Results

The proportion of habitat patches in the largest component (O'), the proportion of habitat area in the largest component (A') and graph diameter (d(G)) all showed transition behavior across the critical thresholds of $P_C = 0.30$ for the 60m threshold distance and $P_C = 0.15$ for the 90m threshold distance. Between $P = 0.05$ and P_C for both threshold distances, the values of both O' and A' were < 0.2 (Figs. 2 and 3 respectively). Both O' and A' exhibited an inflection as they approached P_C, increased sharply across P_C, followed by a second inflection as P increased beyond P_C. As the amount of habitat increased beyond this second inflection, both O' and A' exhibited asymptotic behavior towards a value of 1.0. When O' < 1.0 for both threshold distances, the calculated value of O' was always smaller than the calculated value of A', which was due to the fact that the calculation of O' gives equal weighting to all included patches regardless of area. The graph diameter at P = 0.05 exhibited low values (Fig. 5) for both threshold distances, increased to a maximum at the critical threshold P_C, then monotonically declined towards a value of zero as P increased beyond P_C. Thus graph diameter was maximized and O' and A' experienced rapid rates of change across the critical threshold.

3.2 Real Landscapes, Traditional Metrics P, NP and A'$_{LP}$

The sample landscapes from the Mid-Atlantic region covered a broad range of P (Fig. 6). There were 106 landscapes with $0 < P \leq 0.2$, 147 landscapes with $0.2 < P \leq 0.4$,

102 landscapes with $0.4 < P \leq 0.6$ and 40 landscapes with $0.6 < P < 0.8$. The average value of P was 0.33 (s.d. of 0.18) and the maximum P value was 0.765.

The number of forest patches (NP) ranged from 1 to 1,349, and was maximized in the approximate range of $0.1 < P < 0.4$ (Fig. 7). Structural fragmentation begins when NP > 1, which was a condition satisfied by all landscapes with the exception of one occurrence of NP = 1 (at P = 0.001). Ninety-three percent of the samples had NP > 100. Of the 27 landscapes with NP < 100, 14 occurred when P < 0.1 and 13 occurred when P > 0.4.

The proportion of habitat in the largest contiguous patch (A'_{LP}) indicates the degree of dominance of the largest patch on the landscape. Values of A'_{LP} were observed to take on a wide range of values across the whole P gradient (Fig. 8). The probability of large A'_{LP} values, however, generally increased with P. For example, 96% of the 27 landscapes with $A'_{LP} > 0.9$ had P values greater than 0.55. In contrast 84% of the 268 samples with $A'_{LP} < 0.5$ were in landscapes with P < 0.4. All of the 38 landscapes with $A'_{LP} < 0.1$ occurred in landscapes with P < 0.4. Thus, although there was a great deal of variability among landscapes across all values of P, there were trends in A'_{LP} and NP across the gradient suggesting a decreased probability of the largest patch comprising the majority of habitat.

To summarize the variability of A'_{LP} as a function of P, I divided the landscapes into equal intervals of P = 0.1 and calculated average A'_{LP} values and 95% confidence intervals for each interval (Fig. 9). The average values of A'_{LP} were the same for the intervals for P < 0.3 (average value of $A'_{LP} \sim 0.22$), implying that the average area of the largest patch decreased linearly as P decreased from 0.3 towards 0.0. As the

proportion of habitat increased above 0.3, the average value of A'_{LP} increased monotonically towards 1.0.

The observed values of NP and A'_{LP} both indicated that the majority of sample landscapes were structurally fragmented: 93% had NP > 100 (Fig. 7) and 57% had $A'_{LP} < 0.5$ (Fig. 8). Thus at scale of the sampled landscapes, forest habitat in the Mid-Atlantic region was fragmented to a degree that justified exploring the functional connectivity of landscape mosaics that form by virtue of a species' ability to cross gaps. The landscape with NP = 1 was dropped from further analysis because no changes in graph metrics would be observable for this sample.

3.3 Real Landscapes, Graph Metrics Related to the Largest Ordered Component

No landscapes had a value of O' = 1.0 for the smallest threshold distance of d_t = 120m, indicating that even for landscapes with P > 0.6 some patches remained isolated from the largest component. The proportion of landscapes with $O' \approx 1.0$ increased with increasing threshold distance (Fig. 10), indicating that increased gap crossing ability essentially connected patches into one large, fully connected component. The proportion of habitat at which occurrences of $O' \approx 1.0$ steadily decreased with increasing threshold distance, indicating that landscapes at P values that are fragmented for species with smaller gap crossing abilities become connected for species with larger gap crossing abilities.

LOWESS regression curves of the calculated values of O' across the P gradient generally indicated minima towards lower values of P and maxima towards the highest values of P for all six threshold distances (Fig. 10). However there was a large amount of variation in O' across all P values, especially for $d_t < 990$m. For

threshold distances of d_t = 120 and 180m (Figs. 10 A and B respectively) the LOWESS regression showed a region of relatively constant O' for P < 0.2, a monotonic increase in O' between 0.2 < P < 0.6, followed by less rapid increases for P > 0.6. For d_t = 360m, LOWESS regression indicated a monotonic increase in O', and a sharp inflection at P $\approx$ 0.3, followed by asymptotic behavior of O' towards 1.0. Similar behavior of the LOWESS regression for O' as a function of P was observed for d_t = 450, 990 and 1,500m (Figs. 10 D, E and F respectively), with the proportion of habitat at which the inflection (monotonic increase transitioning to asymptotic behavior) in the regression curve being reduced with increasing threshold distance. Overall, the behavior of O' versus P (Fig. 10) followed the general trends observed for neutral random maps (Fig. 3).

The proportion of habitat contained in the largest component, A', typically exceeded the proportion of patches contained in the largest component (except when they both equaled 1.0). I found that it was not uncommon for landscapes to have A' > 0.99 and O' < A' across the entire P gradient, a trend that was also observed in random landscapes (Figs. 3 and 4). A landscape with O' < 1.0 may be considered as not functionally connected, as the entire collection of patches on the landscape are not part of a single network. However, a landscape with A' > 0.99 would be considered well connected in terms of area, because a majority of habitat is included in the network, even if all patches are not. The extraneous patches (those whose inclusion would force O' and A' to 1.0) represent an insignificant proportion of the habitat. Taking the difference between O' and A' in each landscape showed that, depending on the threshold distance, as many as 40% of the landscapes in which almost all

habitat area was in the largest component had a substantial number of isolated patches. For d_t = 120m, O' was substantially less than 1.0: the average value of O' was 0.68 (s.d. = 0.19). For larger threshold distances the landscapes were primarily connected, with O' > 0.9 in all cases.

The proportion of aggregate area in the largest ordered component relative to the proportion of area contained in the largest patch (η) was generally > 1.0, indicating that the largest ordered component contained a greater proportion of habitat than did the largest patch alone. When $\eta < 1.0$, the largest ordered component did not contain the largest patch. The number of occurrences where the largest ordered component did not contain the largest patch ($\eta < 1.0$) was 40, 20, 8, 8, 5 and 2 for threshold distances of 120m, 180m, 360m, 450m, 990m and 1,500m respectively. Landscapes with $\eta < 1.0$ typically had low P; for example, the mean P for all 40 landscapes with $\eta < 1.0$ for d_t = 120m was 0.15 (s.d. = 0.17). There was, however, one occurrence of $\eta < 1.0$ for d_t = 120m with P = 0.658. At the largest threshold distance the 2 occurrences of $\eta < 1.0$ occurred at P = 0.049 and P = 0.334.

The proportion of area in the largest component relative to the proportion of area in the largest contiguous patch showed maxima consistently in the range $0.1 < P < 0.4$ for all threshold distances (Fig. 12), the same range in P for which the number of patches was maximized (Fig. 7). For P > 0.6 there appeared to be little change in the magnitude of η with increasing threshold distance, indicating that for landscapes with large amounts of habitat contained in the largest patch (i.e., $A'_{LP} > 0.9$, Fig. 8) relatively little habitat is available outside of the largest patch. For P > 0.6 and for

$A'_{LP} < 0.9$ (Fig. 8) the invariance of η indicated that satellite patches were in close proximity to the largest patch. If isolated patches are in close proximity, large gains in area are possible with even small gap crossing ability, which is corroborated by the fact that 88% of the 40 landscapes with $P > 0.6$ had $A' > 0.9$ at the smallest threshold distance of $d_t = 120$m (Fig. 11A). LOWESS regression indicated a trend towards decreased values of η with decreasing P for $P < 0.2$ (Fig. 12), although the magnitude of η could still be rather large for $P < 0.2$. This trend was due to increased distances among patches as P tended towards 0.0, which was corroborated by the fact that values of η for $P < 0.2$ were generally larger with increased threshold distance.

Graph diameters (d(G)) were smallest at both high and low values of P. Maximum values occurred within different P ranges for different threshold distances (Fig. 13). In general, peak d(G) values occurred within smaller P ranges for increased threshold distance. For example, for $d_t = 180$m (Fig. 12B), d(G) was maximized in the approximate range $0.2 < P < 0.3$, while for $d_t = 450$m (Fig. 12 D) d(G) was maximized in the approximate range $0.1 < P < 0.2$.

3.4 Real Landscapes, Critical Thresholds Defined

Threshold phenomena in landscape pattern are often described in terms of percolation frequency (e.g., Gardner & O'Neill 1990; With 1999) or illustrated as non-linear behavior of metrics related to the size of habitat clusters, or components (e.g., Keitt et al. 1997). I chose to define threshold phenomena in terms of the latter. Because thresholds are related to the size of the largest component (O' and A'), percolation, or map spanning ability is not a necessary requirement for connectivity. Random map

results showed rapid nonlinear changes in the proportional order, O' (Fig. 3) and area A' (Fig. 4) of the largest component at P_C values at which d(G) was maximized (Fig. 5). Nonlinear changes of O', A' and d(G) across P_C represent transitions from an "unconnected state" to a "connected state".

Results from forested landscapes showed that nonlinear changes in O' (Fig. 10) and A' (Fig. 11) occurred across P values at which d(G) was maximized (Fig. 13), similar to the trends observed for random maps. To determine threshold habitat proportions, the peak in d(G) was defined by the maximum value of the LOWESS regression curve (Fig. 13). The value of P associated with the peak value of d(G) was then designated as the critical proportion of habitat, P_C, for each threshold distance.

Thresholds require testing to see if they differentiate between a state of "un-connected" for $P < P_C$ and "connected" for $P > P_C$. For illustrative purposes, a landscape was considered connected if 80% of patches were contained in the largest component (i.e., $O' > 0.8$) or if 80% of available habitat was contained in the largest component (i.e., $A' > 0.8$). The choice of 0.8 was arbitrary, but the selection of a user-defined cutoff is consistent with accepted methods for defining thresholds (Stauffer 1985; With 1999). The proportion of landscapes satisfying the condition of $O' > 0.8$ or $A' > 0.8$ illustrates the probability that the largest component contains a preponderance of available patches or habitat respectively. If the thresholds effectively discriminate between "connected" and "unconnected" states, then the probabilities should be higher for $P > P_C$ for both O' and A'. The probabilities of both $O' > 0.8$ (Table 4) and $A' > 0.8$ (Table 5) were higher for landscapes with $P >$

P_C. The differences between probabilities (above and below P_C) for O' and A' were greatest for threshold distances of 180m, 360m and 450m.

At d_t = 120m, 69% of the landscapes with $P > P_C$ (0.312, Table 5) had more than 80% of available habitat connected within the largest component, while only 18% of those same landscapes contained greater than 80% of patches (O' > 0.8). As threshold distance increased from 120m to 1,500m, the probabilities of both O' > 0.8 and A' > 0.8 for $P > P_C$ generally increased, indicating that forest habitat generally became more connected at smaller proportions of habitat as threshold distance increased. The probabilities of O' > 0.8 and A' > 0.8 for $P < P_C$ also increased with increasing threshold distance. At d_t = 1500m, the probabilities were on the order of 70% for both O' and A' for $P < P_C$.

3.5 Real Landscapes, Graph Metrics Related to Overall Landscape Connectivity

The normalized number of components (NC') is a measure of the number of components relative to NP. If there are many isolated patches, NC' is small, whereas if the landscape contains a small number of large networks that include a majority of patches on a landscape, NC' approaches 1.0. The value of NC' generally increased monotonically at smaller threshold distances (Fig. 14 A, B). For a given proportion of habitat, NC' increased with increasing threshold distance for each sample landscape (Fig. 14). LOWESS regression curves showed a monotonic trend for threshold distances of d_t = 120 and 180m, but no inflections characteristic of critical thresholds in P. For larger threshold distances, the preponderance of landscapes had NC' values very close or equal to 1.0.

The gamma index (γ) measures the number of edges (connections) in a landscape relative to the number of edges in a fully connected planar graph with the same number of patches. When plotted against P, the gamma index showed a slight monotonic increase from lowest to highest amounts of habitat for threshold distances d_t = 120 and 180m (Figs. 14A and 14B). Values of the gamma index did not approach 1.0 until d_t = 360m and $0.2 < P < 0.5$ (Fig. 15C). It was not until d_t = 990m that the majority (i.e., >90%) of the landscapes had $\gamma > 1.0$.

Chapter 4: Discussion

Movement of organisms among populations is a critical ecological process. Where individual, isolated populations may suffer high local extinction probabilities, sufficient movement of individuals among populations can allow an entire network to persist via metapopulation dynamics (e.g., Lande 1987; Levins 1969, 1970). As habitat is lost and fragmented, understanding the degree to which structurally fragmented landscapes are functionally connected becomes increasingly important. Many factors affect the likelihood of functional connectivity among patches on a landscape, including the behavioral characteristics of an organism, but the distances among patches relative to a species' gap crossing ability ultimately defines connectivity. Graph theory provides a framework that implicitly assesses connectivity based on these gap-crossing abilities.

4.1 Graph Metric Evaluation on Random Neutral Landscapes

Graph metrics related to the size (order, area and diameter) of the largest component had characteristic forms as a function of habitat proportion (P) on random landscapes. Using closest edge distances measured pixel centroid-centroid, connection patterns formed for threshold distances (60m and 90m) that were equivalent to that formed by programs such as RULE (Gardner 1999) using the 12 and 24-neighbor rules respectively. By this I mean that the proportion of patches (O'), the proportion of habitat (A') and the graph diameter (d(G)) of the largest component exhibited threshold behavior across critical proportions of habitat (P_C) predicted by percolation theory (Plotnick & Gardner 1993). The study of threshold phenomena on graph

structures is considered a general extension of traditional lattice percolation analysis (Keitt et al. 1997). Studies of percolation phenomena as a function of variable threshold distances have been performed for real landscapes with fixed proportion of habitat (P) (Bunn et al. 2000; Keitt et al. 1997; Urban & Keitt 2001). The random map results presented in this thesis are the first illustration of the variation of graph metrics in response to both variable P and threshold distance.

Graph diameter is a measure of the matrix distance traversed to travel between the two furthest patches that define the maximum eccentricity of a landscape graph (Urban & Keitt 2001). Because there may be multiple stepping stone pathways between the two furthest patches, the distance from one "side" of the component to the other will vary depending on the route taken. Graph diameter is the shortest routing between the furthest patches (Urban & Keitt 2001). In random maps, P_C indicates the smallest P (and maximum amount of non-habitat, or matrix) at which the largest component reaches the linear dimension of the map and percolates. The route taken by a percolating cluster is tortuous (Stauffer 1985) and at P_C involves the maximum amount of matrix to be traversed to span the map. Because d(G) directly measures the total sum of matrix distances traversed, and because these distances are maximized at P_C, the graph diameter is necessarily maximized at P_C (Fig. 5).

The graph diameter tends towards 0.0 on either side of P_C (Fig. 5). For $P < P_C$, d(G) decreases towards 0.0 because the size of the largest component tends to be reduced as P tends towards 0.0. For $P > P_C$, the graph diameter decreases as the pathways across the largest component become more direct and the amount of matrix decreases

as more area is occupied by habitat. In the limiting case d(G) = 0.0 at P = 1.0 because there is no matrix to traverse.

The relationship between the graph diameter and P was not expected. Urban & Keitt (2001) considered graph diameter to correspond to the radius of gyration (R). The radius of gyration actually measures a fundamentally different attribute of the largest component than the graph diameter. The radius of gyration is a measure of the average distance a randomly placed organism would have to move to reach the component "boundary" (Stauffer 1985). The boundary is defined by an imaginary ring with radius R centered on the centroid of the largest component (Stauffer 1985). As such, R is a function of the size and configuration of the largest component that reaches maximum values at P_C (similar to both O' and A'). In contrast R is maximized when P = 1.0 (e.g. Neel et al. 2004). Different patch configurations may yield equivalent R while providing different d(G) values. The smaller the value of d(G) the greater the expected flux of organisms among patches within the largest component (Bunn et al. 2000; Johnson 1988; Sutherland et al. 2000; Urban & Keitt 2001). Graph diameter is thus ecologically relevant in a manner not embodied by the radius of gyration.

4.2 Fragmentation and Connectivity in the Mid-Atlantic Region: Metrics Related to the Largest Ordered Component

Forest habitat in the Mid-Atlantic region was highly structurally fragmented at the scale of the sampling scheme (Figs. 6 and 7). Variability in NP and A'_{LP} at any particular value of P indicated a wide range of structural fragmentation across the entire gradient of $0.0 < P < 0.8$. The degree to which structural fragmentation affects

a species is dependent on the distances that separate patches, the nature of the intervening matrix and the ability of the species to cross gaps. A landscape is fully connected (i.e., O' = 1.0) for a species if all patches are part of one, large network of patches (Bunn et al. 2000; D'Eon et al. 2002; Dunn 1991; Keitt et al. 1997; Urban & Keitt 2001). None of the sample landscapes were fully connected for threshold distances of d_t = 120m and d_t = 180m (Table 3), suggesting that much of the Mid-Atlantic region is functionally fragmented for species unable to cross gaps ≥ 180m (e.g. Tables 1 and 2). In contrast, 78% of the sample landscapes had O' = 1.0 for d_t = 1500m, suggesting that much of the region was functionally connected for organisms able to traverse at least that distance.

Landscapes may be, for all intents and purposes, functionally connected if 99% of habitat area is within the largest component. Because A' increases at a faster rate with increasing P than does O' (Figs. 3, 4, 10, 11), between 9% and 40% of the sample landscapes (Table 3) were very well connected in terms of area (A' > 0.99) even when they were not fully connected in terms of O'. This discrepancy between O' and A' is important. If O' < 1.0 for a species with a specific d_t, many approaches would consider the landscape to be functionally fragmented regardless of how much habitat area was contained in the largest component (e.g., Bunn et al. 2000; D'Eon et al. 2002; Dunn 1991; Urban & Keitt 2001). However, if 0.99 < A' < 1.0 at the same d_t, patches excluded from the largest component would not add much to the habitat available for species with larger d_t and for which O' = A' = 1.0. How valuable are these "added" patches that connect to the largest component for species with larger d_t? Methods are available to assess the value of such "added" patches, and in the

following section I outline a process that takes advantage of the discrepancy between O' and A' to accomplish the same goal but with far fewer computations.

4.2.1 Utilizing the Discrepancy Between O' and A'

Conservation applications of graph theory often involve sensitivity analyses to determine which patches are of least value to metapopulation dynamics (e.g., Bunn et al. 2000; Keitt et al. 1997; Urban & Keitt 2001). I propose that the discrepancy between O' and A' can provide information on which patches are of least value to a spatially structured population, specifically for situations in which $A' \approx 1.0$ and $O' < A'$. For example, a hypothetical landscape has 3 patches; 2 of which are connected (O' = 0.66) by a distance of 100m and containing 99% of available habitat ($A' \approx 1.0$); the third patch represents 1% of the available habitat and is separated by 200m from the closest of the two connected patches. By the requirement that O' = 1.0 for full connectivity, this hypothetical landscape would be fully connected for a species with threshold distance d_t = 200m and functionally fragmented for a species with d_t = 100m. However, this landscape is very well connected with $A' \approx 1.0$ for both threshold distances. The outlying patch, if connected, would most likely act as a sink rather than a source, and its loss would not result in appreciable declines of A'.

Although the previous example was simplistic, the situation becomes less clear when there are hundreds or thousands of patches. Previous researchers (Bunn et al. 2000; Urban & Keitt 2001) have analyzed landscapes with fixed P, varied the threshold distance, and considered the critical d_t to be that at which full connectivity, O' = 1.0, was achieved. Bunn et al. (2000) and Urban & Keitt (2001) assessed the importance

of individual patches to overall metapopulation dynamics by calculating the dispersal flux and traversability of the fully connected landscape(s). Dispersal flux (F) is an area and distance weighted sum of the interactions among all patches on a landscape. Traversability (T) is the equivalent of the graph diameter. An "Importance Index" (e.g. Keitt et al. 1997) can be calculated for each patch by removing that patch, recalculating F and T, and dividing the new values by those calculated for the original landscape.

Importance indices quantify the value of individual patches to the whole, but require re-analysis of as many graph configurations as there are patches on the landscape (possibly thousands of graph analyses). In the special case where $A \approx 1.0$ at d_t less than the critical threshold distance, it is possible to streamline the analysis by the following process: determine the threshold distance at which $A' \approx 1.0$, $d_t(A)$; determine the critical threshold distance at which $O' = 1.0$, $d_t(O)$; and identify those patches in the fully connected landscape at $d_t(O)$ that were not included in the largest component at $d_t(A)$. The identified patches represent a minor proportion of habitat and are relatively isolated, therefore their importance index with respect to F would be small. Thus $d_t(A)$ is a secondary critical threshold distance required for the landscape to be well connected ($A' \approx 1.0$) even though it is not fully connected (i.e., $O' < 1.0$). Definition of the secondary critical threshold distance identifies those patches of least importance to the metapopulation and that do not serve as stepping-stones. The process I proposed makes use of metric versus threshold distance curves that can easily be generated (Bunn et al. 2000; Urban & Keitt 2001), and does not

require re-analysis of as many landscape graph configurations as there are patches on the landscape, which could be cumbersome if thousands of patches are involved.

Further information on the value of the patches that were not included in the largest component at $d_t(A)$ can be obtained by observing the behavior of the graph diameter. Comparison of d(G) at $d_t(A)$ and $d_t(O)$ would indicate the relative contribution of the identified patches to traversability, which has been linked to the concept of long distance rescue effects (Urban & Keitt 2001). If d(G) is appreciably increased by the addition of identified patches, the implication is that these patches are spread over a wide geographic area and could "rescue" the main body of the component if it were affected by disturbance (Levins 1969), which may be important for rare or endangered species. Thus the outlying patch(es) may not be necessary for short-term population persistence, but may be useful for recovery from infrequent but broad scale disturbance. Determination of their long-term value would require a population viability analysis. If d(G) is not increased, the interpretation is that these patches are added to the main component as "end-nodes" (e.g., Urban & Keitt 2001), located around the periphery of the main body of the largest component. Bunn et al. (2000) and Urban & Keitt (2001) showed that for their focal landscapes, sequential end-node removal had minimal effect on traversability compared to other patch removal schemes. Their results are supported by percolation theory, as the main path taken by the graph diameter is analogous to the "backbone" of a percolating cluster. At the critical threshold percolating clusters have a preponderance of "dangling bonds" (Stauffer 1985), which are the equivalent of end-nodes. The removal of dangling bonds does not affect the integrity of the percolating cluster backbone, just as removal

of end-node patches does not appreciably reduce the traversability of the largest component.

4.2.2 Does the Largest Component Include the Largest Patch?

The "largest component" is defined as the network with the largest number of internally connected patches. Analysis of real landscapes showed that a consequence of defining the largest component in such a manner is the possible occurrence of networks with aggregate area less than that of the largest patch (i.e., $\eta < 1.0$). If landscapes are not considered to be connected until O' = 1.0 (e.g., Bunn et al. 2000; Urban & Keitt 2001) then there is no risk of $\eta < 1.0$. However, if land managers are interested in a particular landscape that is fragmented at scales that impact a focal organism (O' < 1.0), there is a risk of the largest component having $\eta < 1.0$. At the smallest threshold distance (d_t = 120m) roughly 10% of the forested landscapes had $\eta < 1.0$, while at the largest threshold distance (d_t = 1500m) less than 1% of the landscapes had $\eta < 1.0$. Ideally the largest patch would be connected within the largest component, acting as a source (e.g. Etienne & Heesterbeek 2001), but if the largest component excludes the largest patch, conventional wisdom generally dictates preservation of the largest patch (e.g. Etienne 2004). Thus management may shift from preservation of a network to preservation of the largest patch if $\eta < 1.0$.

4.2.3 Empirically Determined Critical Thresholds in P

Critical thresholds in the proportion of habitat imply that the effects of fragmentation on connectivity, and ultimately on species persistence, are non-linear (e.g., Andrén 1994; Gardner et al. 1987). At and below the critical threshold the effect of patch

isolation and reduced patch size can lead to population declines at rates not accounted for by habitat loss alone (e.g., Lindenmayer & Luck 2005; Monkkonen & Reunanen 1999). Connectivity among patches is a function of the biology of individual species and their inherent gap crossing ability; therefore a single threshold does not adequately describe the response of all species in a landscape to changes in habitat amount and pattern (e.g., Bascompte & Rodriguez 2001; Gardner & O'Neill 1990; With & Crist 1995).

Percolation theory can differentiate between threshold P_C values for species with different gap crossing abilities (e.g., With 2002a). Random map percolation thresholds have been used to assess the connectivity of contiguous forest (Riitters et al. 2000; Riitters et al. 2002; Wade et al. 2003), but applying random map thresholds for species with gap crossing ability may be problematic. Plotnick & Gardner (1993) showed that percolation based P_C values on random maps tend towards 0.0 as gaps exceed 8 pixels, or 270m at the scale of the forest data (measured pixel centroid-centroid). The alternatives to random neutral landscapes are hierarchical models. Hierarchical neutral landscapes (O'Neill et al. 1992) reflect the inherent patch structure of natural landscapes. O'Neill et al. (1992) and With (1999) showed that percolation thresholds for hierarchical maps with varying levels of contagion had smaller P_C values than their random map counterparts.

The results from real landscapes (e.g. Figs. 10, 11 and 13), however, show that random neutral map threshold predictions may be inappropriate for assessment of real landscapes, and that the deviations of thresholds from those predicted from neutral models increase with increasing threshold distance. For example, d_t = 180m

(measured pixel centroid-centroid) represents a gap crossing ability of 5 pixels. Percolation simulations would model d_t = 180m with a 60-neighbor rule, which for random maps has P_C = 0.066 for lattice grids (Plotnick & Gardner 1993). The proportional order and area (Figs. 9B and 10B respectively) were less than 0.6 for the majority of sample forested landscapes with $P < 0.2$, or three times the predicted P_C. Deviations of results from random map predictions increased with increasing threshold distance. Therefore random map percolation thresholds were not an effective indicator of connectivity thresholds when large gap crossing abilities were considered.

Because percolation thresholds from random maps were not appropriate for real landscapes, I used the characteristic behavior of the graph diameter across gradients in P to empirically estimate P_C. The graph diameter was maximized for a fixed threshold distance at P_C on random landscapes (Fig. 5) in much the same way it was maximized for landscapes with fixed P at a critical threshold distance (Bunn et al. 2000; Urban & Keitt 2001). The maximization of d(G) at critical thresholds is thus useful for identification of such thresholds. Using this feature of the graph diameter, P_C values were associated with the maximum value of the LOWESS regression for each threshold distance (Figs. 12A-12F). Probabilities were generated to assess how well these thresholds differentiated between states $O' > 0.8$ for $P > P_C$ versus $P < P_C$ (Table 4) and $A' > 0.8$ for $P > P_C$ versus $P < P_C$ (Table 5). Using a cutoff value of 0.8 for O' and A' thus decoupled connectivity from the strict percolation requirement, and provided a method for analyzing connectivity independent of map spanning ability. The cutoff value of 0.8 was arbitrary but served the purpose of illustrating the

method, and was consistent with the accepted method of user-defined cut-offs for identification of thresholds (Stauffer 1985; With 1999).

Thresholds defined for the proportional order most clearly differentiated between "connected" and "unconnected" states for d_t = 360m at P_C = 0.146 (Table 4). Landscapes with P > 0.146 had a 76% probability of O' > 0.8 while landscapes with P < 0.146 only had a 20% probability of O' > 0.8. The probabilities had less of a discriminatory ability for threshold distances smaller and larger than 360m. At d_t = 120m, only 20% of the landscapes had O' > 0.8 above P_C = 0.312 (Table 4), compared to 0.5% below. An obvious reason for this lack of differentiation was that very few landscapes had O' values approaching 1.0 at this threshold distance (Fig. 10A). At the largest threshold distance, d_t = 1500m, 97% of landscapes with P greater than P_C = 0.124 (Table 4) had O' > 0.8, compared to 68% below.

The large proportion of landscapes with O' > 0.8 for P < 0.124 (at d_t = 1500m) may be due to the fact that species with gap crossing ability on the order of 10% of the linear scale of a map simply have a very high probability of "perceiving" a landscape to be well connected regardless of habitat arrangement. Such a situation may be due to an "undersized map" as described by Gardner et al. (1987), where map scales small relative to the connectivity criteria yield disproportionately large probabilities of high levels of connectivity.

Connectivity based on the proportional area (A') was most clearly differentiated at P_C = 0.266 for d_t = 180m (Table 5). Landscapes with P > 0.266 had a 75% probability of A' > 0.8 while landscapes with P < 0.266 only had an 11% probability of A' > 0.8. Unlike O', the proportional area had a greater ability to differentiate for the smallest

threshold distance of d_t = 120m (69% versus 7% above and below P_C respectively, Table 5, compared to 20% and 0.5% respectively for O', Table 4). The greater threshold differentiation for A' versus O' at the smallest threshold distance was attributed to the characteristic behavior of A' > O' across the entire P gradient. Similar to the probabilities defined for O', the proportional area had decreasing discriminatory ability as threshold distances increased to 1500m.

The varying ability of the thresholds to discriminate between states of connectedness (Tables 4 and 5) indicates scale dependency. Connectivity, specifically the determination of thresholds, must be assessed at multiple scales (e.g., Gardner & O'Neill 1990; With 1999). Here I assessed connectivity across multiple gap crossing scales, but the validity of thresholds in P defined in this work must be verified by further testing across multiple extents and grain sizes as well. Thresholds will also vary with habitat type, geographic region, and pattern of habitat loss. For example, structural fragmentation is often expected to accelerate below the percolation threshold P_C = 0.5928 predicted for random maps (Gardner et al. 1987; Riitters et al. 2000; Riitters et al. 2002; Wade et al. 2003), but Ferraz et al. (2005) showed that portions of the Amazon forest in Brazil exhibited accelerated fragmentation at a much lower critical threshold, P_C = 0.35. The lower critical threshold observed for the Brazilian forest was due to aggregated patterns of clear cutting. Because fragmentation thresholds vary, connectivity thresholds will also vary depending on the overall patterns of habitat loss. The differing ability for P_C to differentiate connectivity status based on O' and A' suggest different thresholds may exist depending on which criteria is sufficient for good connectivity.

The connectivity thresholds presented here should not be misconstrued as endorsement of P_C values as targets for management of forest habitat in the Mid-Atlantic region. Instead, the results indicate that the method may provide land managers a means for ranking landscapes in terms functional fragmentation (poor connectivity) risk at multiple gap crossing scales. Such a risk analysis would allow land managers to focus on those landscapes with $P < P_C$ as most at risk of functional fragmentation in much the same way that percolation thresholds have been used to identify geographic regions most at risk of structural fragmentation (Riitters et al. 2000; Riitters et al. 2002; Wade et al. 2003). Assigning risk based on P_C values would allow land managers to focus on those landscapes most likely to be poorly connected. Such an assessment could be a first step in "tactical monitoring" of broad geographic regions (Urban 2001).

4.3 Fragmentation and Connectivity in the Mid-Atlantic Region: Metrics Calculated for the Whole Landscape

Metrics related to the largest component provide useful information on how varying threshold distance can change the size of the largest cluster of connected patches. But within a landscape, other components exist as well. When multiple components exist, each component is scaled to the gap crossing ability of a species, such that the patches within a component should behave similarly over time compared to patches contained in different components (Urban 2005). Thus, graph components are analogs of "patches", just as the proportion of habitat in the largest component, A', is roughly analogous to the proportion of habitat in the largest patch, A'_{LP}. Therefore the number of components (NC) indicates the total number of *groupings of connected*

patches (components), which are isolated from other components on the landscape. In the limiting case where all patches are parts of one large connected network, NC = 1.

The metric NC' is a normalized measure of NC with values close to 1.0 indicating higher levels of connectivity. A general monotonic increase in NC' with increasing P was observed for d_t = 120m and 180m, but NC' was relatively insensitive to proportion of habitat for larger threshold distances (Fig. 14). While the proportional order of the largest component may still be small when NC' $\approx$ 1.0, larger values of NC' indicate a higher level of overall connectedness. For example, a landscape may contain 1,000 patches arranged in 8 separate components, the largest of which contains 300 patches (O' = 0.3). If each of the remaining seven components contain 100 patches, NC' = 0.992. So NC' can indicate a "well connected" landscape in the sense that there are far fewer components than patches, even if the largest component only includes 30% of those patches. Thus NC', coupled with O' and A', provides information on the size distribution of components in a landscape in much the same way as NP and A'_{LP} provide complementary information on the size distribution of patches in a landscape. The relatively constant values of NC' $\approx$ 1.0 across P for dt > 360m (Fig. 14) indicates that landscapes in the Mid-Atlantic region with several hundred or more patches generally coalesced into a very small number of components when O' < 1.0. Values of NC' < 1.0 for all landscapes at d_t = 120m (Fig. 14) corresponds to the fact than none of these landscapes were fully connected (O' = 1.0, Fig. 10).

For management purposes, it may even be desirable to maintain a small number of patch networks (components) where each network is isolated from the others, a condition satisfied when O' < 1.0 and NC' ≈ 1.0. If long-term persistence in each component were a sufficiently high probability, each component would support a population. The lack of connectivity among components may serve to check the spread of disease or invasive species that may be detrimental to overall persistence in the landscape (e.g., With 2002b). Sufficient isolation of each component may assure that if disturbance destroys one population, other populations may be unaffected. The purpose is not to argue that isolated populations are desirable, rather to illustrate that for relatively abundant species, full connectivity of all habitat may not always be necessary or even beneficial for long-term persistence at the landscape scale.

A second metric related to whole landscape connectivity was the gamma index (γ), which has been explored in a limited number of landscape contexts (e.g., Acosta et al. 2003; Forman 1995; Ricotta et al. 2000). This index is a measure of the complexity of connectedness of a landscape relative to a hypothetical planar graph with an equivalent number of patches. A planar graph is a fully connected graph (O' = 1.0) that has an optimized connection pattern among patches such that removal of single patches will have minimal effect on connectivity (e.g., Ricotta et al. 2000). As γ approaches 0.0, even for a fully connected landscape (O' = 1.0), the degree (the number of edges, or connections) of each patch generally decreases. Low γ values correspond to linear chains, meaning that removal of patches in the middle of the chain could disconnect the landscape. As the gamma index increases towards 1.0, the degree of each patch generally increases, indicating a multiplicity of pathways among

all patches in the landscape. As the gamma index exceeds 1.0, increasing redundancy in routing paths among patches ensures that connectivity is less sensitive to patch removal. The gamma index does not identify which patches within a landscape would disrupt connectivity if removed (called "cut-nodes"); rather the magnitude of γ signifies the likelihood of disrupting connectivity with removal of a single patch.

4.4 Graph Metric Degeneracy with Respect to P

All landscape metrics suffer from degeneracy, and graph metrics are no exception. Degeneracy occurs when a metric yields multiple values for the same value of a supposedly controlling variable, in this case P (in which case it is implicit that equivalent metric values can occur for multiple P values as well). Degeneracy with respect to P means that the metric cannot differentiate between different habitat configurations, which occurs because information is necessarily lost when a single number is used to describe complex phenomena. All of the graph metrics calculated for real landscapes were degenerate to some degree (Figs. 9-14). For example, different landscapes with the same P, number of patches and equivalent O' can have different values of A', d(G), NC and γ, making O' alone a poor indicator of landscape configuration. In addition, the interpretation of graph diameter is different on either side of P_C (Fig. 5). Degeneracy of landscape metrics also explains why critical thresholds in habitat proportion cannot be used to say with certainty that landscapes are connected based on P alone; landscapes can be fully connected below P_C and poorly connected above P_C. Therefore the proper use of critical P thresholds is risk assignment; landscapes with $P > P_C$ are *more likely* to be well connected than landscapes with $P < P_C$.

Jaeger (2000) proposed eight criteria that are considered necessary for a metric to be a good descriptor of landscape configuration. These criteria were; intuitive interpretation, low sensitivity to small patches, monotonic reaction to different fragmentation phases, detection of structural differences, mathematical simplicity, modest data requirements, mathematical homogeneity, and additivity. An additional desirable metric attribute is the ability to assess changes in landscape configuration that are independent of area (Neel et al. 2004). This ability is particularly important for studies of habitat fragmentation in which disentangling effects of habitat loss from changes in configuration (e.g., aggregation, subdivision, and isolation) of the remaining habitat has been a major goal (e.g., Belisle & Clair 2002; Bender et al. 1998; Fahrig & Jonsen 1998; Fahrig & Merriam 1985; Trzcinski et al. 1999).

Metrics calculated for the largest component (O', A' and d(G)), are intuitive, simple, and have modest data requirements. All three metrics are sensitive to small patches. Values of O' and A' at any P are a function of configuration only, and are thus sensitive to structural differences independent of area. The proportional order and area exhibit monotonic reactions within different fragmentation phases (on either side of or across P_C). Graph diameter is truly degenerate because it provides similar values on either side of P_C (Fig. 5), but the behavior on either side of P_C is monotonic. None of the 3 metrics (O', A' and d(G)) are additive, in that values calculated for a landscape are not the sum of values calculated for any two landscapes that were created by bisecting the original. Metrics calculated for the entire landscape (NC' and γ) are simple, have modest data requirements, and are not additive.

Thus graph metrics suffer from the same drawbacks as all other landscape pattern metrics. However, all is not lost. The graph metrics do convey important information specific to landscape connectivity that is not obtainable from the traditional suite of landscape pattern metrics found in programs such as FRAGSTATS (McGarigal et al. 2002). Interpretation of graph metrics must take into account unique features of the focal landscape (which is true of all landscape pattern metrics). If all of the tested metrics are calculated for a landscape and analyzed simultaneously, far more information will be provided to discriminate between habitat configurations than if any single metric was investigated on its own. In addition, graph analysis allows for visualization landscape networks (e.g., Bunn et al. 2000; Keitt et al. 1997; Urban & Keitt 2001), which helps provide a visual basis for intuitive understanding of the graph metrics.

4.5 Limitations of the Analysis

This work has made use of two assumptions and two decisions that were adopted to simplify the analysis while keeping true to the main goal of illustrating and explaining the behavior of graph metrics across gradients in habitat proportion. These choices do not affect the general trends, but would have limitations for management of forests or forest dependent species within the Mid-Atlantic region. The assumptions were that patches were connected by Euclidean shortest path distances and all forest patches were of equal quality. I decided to include all patches (including single pixel patches) and metrics were calculated with equal weighting of all graph edges (connections). All of these limitations can be dealt with in more sophisticated graph theory applications.

Straight-line Euclidean distances are often used in pattern analysis across connectivity scales (e.g., D'Eon et al. 2002; Dale & Rauscher 1994; Keitt et al. 1997; Rudd et al. 2002; Sondgerath & Schroder 2002; Uezu et al. 2005), and are analogous to defining "patches" using extended neighborhood rules that allow gap-crossing ability (Plotnick & Gardner 1993; With 1999, 2002a). However, straight-line distances do not take into account features of the intervening matrix that may influence the actual path an organism travels from one patch to another. Inhospitable matrix may prevent movement among patches even if the patches are closer to each other than the gap crossing distance of a species. Least cost methods assign varying traversal costs to different matrix land cover types, and distances are measured in cost units (e.g., Bunn et al. 2000; Rothley & Rae 2005). Bunn et al. (2000) reported that the topology of landscape graphs was not sensitive to the type of distance measure used except at the scale of large obstacles in the landscape. Thus the use of Euclidean distances was sufficient to capture the topology of the graph metrics as a function of P.

Assuming all forest patches are of equal quality ignores the fact that different patch sizes and geometries, soil types, slope, aspect, water availability, forest types, successional stage, and forest health conditions can affect the carrying capacity per unit area of forest. Assigning a "patch quality" index (e.g., Acosta et al. 2003; Urban 2005) that takes some or all of these factors into account increases the species and landscape specificity of an analysis. Because I was interested in evaluating graph metrics across broad gradients in P, analysis of forest patches in general was appropriate. However analysis using quality weighted forest area would give results more appropriate for species-specific investigations.

Many organisms require patches of a sufficient size (minimum area requirement, MAR) to persist at the patch level (e.g. With 1999). Assessing connectivity for a species with known MAR translates into retaining only those patches large enough to be of ecological significance (e.g., Bunn et al. 2000; Keitt et al. 1997; Rudd et al. 2002; Urban & Keitt 2001). Another useful feature of MARs is that their use can reduce classification errors, which are most prevalent at the scale of map resolution (Keitt et al. 1997). My analysis included all forest habitat for calculation of graph metrics, including single pixel patches. However, in preparation for a separate manuscript, I analyzed the 395 sample landscapes with MARs of 1, 10 and 100ha. The topology of the graph metrics as a function of P was not influenced to any great extent, indicating that the trends in graph metrics are robust. What this means is that the shape of the curves is robust to changes in parameters such as MAR, although the values of the metrics at any P and locations of thresholds, if they exist, may vary.

Finally, a fundamental rule of geography is that all patches within a landscape are interrelated to some extent, but near patches are more related than distant ones. Thus connectivity analysis should, at some level, account for distances among patches with greater weighting to patches in closer proximity. The graph diameter takes this feature into account for the largest component because its value is directly related to the distances among patches. In contrast the gamma index, the measure of "whole landscape" connectivity does not account for different weighting based on proximity: all connections are assigned a value of 1 regardless of the distance involved. An alternative to the gamma index, the Harary index (Ricotta et al. 2000) measures the sum of the inverse distance between all connected patches in a landscape, such that

connections between near patches are weighted higher than distant patches. Normalization of the Harary index, however, has only been analytically derived for landscapes with unit distance between adjacent patches (Ricotta et al. 2000). The Harary index would generally be minimized across the P gradient at the smallest threshold distance and increase to maximum values for each landscape at the largest threshold distance, similar to the gamma index. The utility of the Harary index, compared to the gamma index, is that it has a better ability to discriminate between well connected and poorly connected landscapes at a given P and d_t (Ricotta et al. 2000). Therefore, for individual landscapes, the Harary index may be a more useful measure of connectivity.

Chapter 5: Conclusions and Future Direction

Connectivity among habitat patches is central to species persistence in structurally fragmented landscapes (Taylor et al. 1993). Many approaches are available for quantifying connectivity, but graph theory is considered the most cost-effective for analysis of broad geographic regions (Calabrese & Fagan 2004; Urban 2005). Graph theory can provide initial processing of regional data for identification of critical areas and for development of broad scale management plans (Bunn et al. 2000). As data are collected, graph models can increase in complexity to incorporate features relevant for management of specific species (e.g., Bunn et al. 2000; Keitt et al. 1997; Urban & Keitt 2001). Although graph theory has tremendous potential, its use in landscape applications is still somewhat limited. There are only a small number of applications in the literature, and all of them deal with specific conservation situations with static amounts of habitat. Little information is available regarding the behavior of graph metrics for a wide array of situations that may occur across broad gradients in habitat proportion (P).

This thesis provides the first uniform evaluation of graph metrics for multiple gap crossing scales across gradients in habitat proportion which encompass wide variations in the size of the largest patch and number of patches. Such an evaluation is relevant for interpretation of graph metrics in much the same way that other landscape metrics have been systematically evaluated in the past (e.g., Neel et al. 2004). It is imperative that graph metrics be understood in the context of both habitat proportion and fragmentation if results from future applications are to be interpreted

correctly. Calculation of graph metrics across gradients in P led to observations that have not been reported previously and may be useful for conservation management. Graph metrics have characteristic forms when plotted against P. These forms are useful for interpretation of graph metrics in general and contribute to the overall understanding of landscape graph analysis. Three main conclusions were inspired by the analysis. The first conclusion is that there is a risk that the largest component may consist of many small patches with aggregate area less than that of the largest patch on the landscape. Generally the "largest" component will contain both the largest number of patches and the largest aggregate area, but this cannot be assumed. A second conclusion is that distinctive features of the metrics as a function of P can be used directly for conservation management. One example is that for landscapes that are not fully connected, the magnitude of the proportional order (O') lagged that of the proportional area (A'). This feature of O' and A' was shown to be useful for identification of secondary critical threshold distances for landscapes where A' $\approx$ 1.0. A third conclusion is that graph metrics, specifically those related to the largest component, behave similar to percolation-based metrics related to the size of the largest patch or cluster. The similarities occur because graph analysis of landscape connectivity (on real or neutral maps) is a generalized extension of lattice percolation methods (e.g. Keitt et al. 1997). Therefore as functions of P, the behavior of metrics such as O' and A' can be interpreted in light of more familiar percolation based metrics related to the size (area) of the largest patch. It is well known that the size of the largest patch generally remains large until a certain proportion of habitat is lost, at which point it rapidly fragments, as predicted by percolation theory (Stauffer 1985).

Similarly, the size (O' or A') of the largest component remains large, and functional fragmentation accelerates rapidly once a sufficient proportion of habitat is lost. Because graph metrics are related to percolation metrics, I postulated that they would capture threshold phenomena, which was confirmed by the analysis. The characteristic form of the graph diameter plotted against P can be used to identify such thresholds. Graph diameter maxima at critical thresholds in P identify the smallest amount of habitat at which the largest component achieves its maximum spanning ability, whether or not the largest component actually spans the map. This thesis is the first investigation to demonstrate characteristic behavior of the graph diameter and how it can be used to empirically derive critical thresholds in P for real landscapes where percolation theory may be inappropriate. The critical habitat proportions using this graph-based method, $0.124 < P_C < 0.312$, were within the general range predicted by more complex metapopulation models (e.g., Fahrig & Jonsen 1998; Lande 1987; With & Crist 1995; With & King 1999b) and observed for some applications in real landscapes (e.g., Andrén 1994; Bascompte & Rodriguez 2001; Radford et al. 2005; Villard et al. 1999; With 2002b; With & Crist 1995). Because the only species-specific parameter used in the graph analysis was gap-crossing ability (threshold distance), the similarity of P_C values suggests that of the parameters quantified for a species-specific metapopulation analysis, gap-crossing ability is a controlling factor. The similarity of P_C values also indicates that for initial assessment of a geographic region, a graph analysis using only landscape data and estimates of gap crossing ability may identify thresholds and critical habitat patches that are most likely to be identified by more complex models, as suggested by Urban

(2005). I do not suggest that graph analysis should replace more realistic metapopulation models; rather the second and third conclusions of this thesis highlight the utility of the graph method in rapidly analyzing broad geographic regions to obtain initial estimates of connectivity.

The P_C values identified using the graph method are not intended for conservation management in the Mid-Atlantic region. The value of the method outlined is in the concept. Because the range of gap crossing abilities for species is tremendous, no single threshold can be expected to adequately assess functional fragmentation as a function of P for all species concerned (e.g., Bascompte & Rodriguez 2001; Gardner & O'Neill 1990; With & Crist 1995). When the range of gap crossing abilities exceeds that at which percolation based thresholds (derived from neutral maps) become inappropriate, alternate methods are required. The method proposed using the graph diameter has the potential to be one such method. Thresholds defined using this method require further testing across scales in extent and grain size to determine their validity. One interesting way to do this would be to perform a moving window analysis (e.g., McGarigal et al. 2002; Riitters et al. 2000; Riitters et al. 2002; Wade et al. 2003) of a broad geographic region, calculating graph metrics for each focal pixel and for multiple window sizes. The practicality of a moving window analysis is a function of time and computational resources. Calculations could be reduced if classification was aggregated to a coarser scale and if the number of patches were reduced through use of minimum area requirements.

Appendix 1: Tables

Table 1. Vertebrate species native to the Mid-Atlantic region and their associated gap crossing ability.

Scientific name	Common name	Gap crossing ability (m)	Reference
Cryptotis parva	least shrew	180 to 450	Corry & Nassauer (2005)
Peromyscus leucopis	white-footed mouse	180 to 450	Corry & Nassauer (2005)
Sorex cinereus	masked shrew	180 to 450	Corry & Nassauer (2005)
Certhia americana	Brown Creeper	450 to 900	D'Eon et al. (2002)
Sciurus niger	fox squirrel	450 to 900	Rosenblatt et al. (1999)
Sorex fontinalis	Maryland shrew	450 to 900	www.natureserve.org
Tamiascurus hudsonicus	red squirrel	450 to 900	Sutherland et al. (2000)
Tamius striatus	eastern chipmunk	450 to 900	www.natureserve.org
Crotalus horridius	timber rattlesnake	990 to 1,500	www.natureserve.org
Picoides villosus	Hairy Woodpecker	990 to 1,500	www.natureserve.org,
Sciurus carolinensis	eastern gray squirrel	990 to 1,500	www.natureserve.org

Table 2. Tree species native to the Mid-Atlantic region and their associated gap crossing ability.

Scientific name	Common name	Gap crossing ability (m)	Reference
Acer rubrum	red maple	120 to 180	Dunn, et al. (1991), He & Mladenoff (1999)
Acer saccharum	sugar maple	120 to 180	Dunn, et al. (1991), He & Mladenoff (1999)
Betula alleghaniensis	yellow birch	180 to 360	He & Mladenoff (1999)
Fraxinus americana	white ash	180 to 360	He & Mladenoff (1999)
Picea glauca	white spruce	180 to 360	He & Mladenoff (1999)
Pinus resinosa	red pine	180 to 360	He & Mladenoff (1999)
Pinus strobus	white pine	180 to 360	He & Mladenoff (1999)
Carya spp.	hickories	990 to 1,500	He & Mladenoff (1999), Sork (1983)
Quercus spp.	oaks	990 to 1,500	He & Mladenoff (1999), Sork (1983)

Table 3. The percent of fully connected forested landscapes (O'=1.0) and well connected landscapes (A' > 0.99) for each of the six threshold distances. The difference indicates how many more landscapes were well connected versus fully connected for each threshold distance

Threshold distance (m)	**Percent of landscapes with O' = 1**	**Percent of landscapes with A' > 0.99**	**Difference**
120	0	10	10
180	0	10	10
360	10	46	36
450	18	58	40
990	69	83	14
1,500	78	87	9

Table 4. Probability of the normalized order of the largest component (O') having a value greater than 0.8 for landscapes with P above and below P_C for six threshold distances.

Threshold distance (m)	**P_C**	**Number of landscapes with $P > P_C$**	**Probability of O' > 0.8 for $P < P_C$**	**Probability of O' > 0.8 for $P > P_C$**
120	0.312	198	0.005	0.18
180	0.266	239	0.019	0.44
360	0.146	325	0.20	0.76
450	0.146	325	0.31	0.86
990	0.128	336	0.59	0.95
1,500	0.124	338	0.68	0.97

Table 5. Probability of the normalized area of the largest component (A') having a value greater than 0.8 for landscapes with P above and below P_C for six threshold distances.

Threshold distance (m)	**P_C**	**Number of landscapes with $P > P_C$**	**Probability of A' > 0.8 for $P < P_C$**	**Probability of A' > 0.8 for $P > P_C$**
120	0.312	198	0.07	0.69
180	0.266	239	0.11	0.75
360	0.146	325	0.26	0.84
450	0.146	325	0.44	0.88
990	0.128	336	0.71	0.95
1,500	0.124	338	0.75	0.96

Appendix 2: Figures

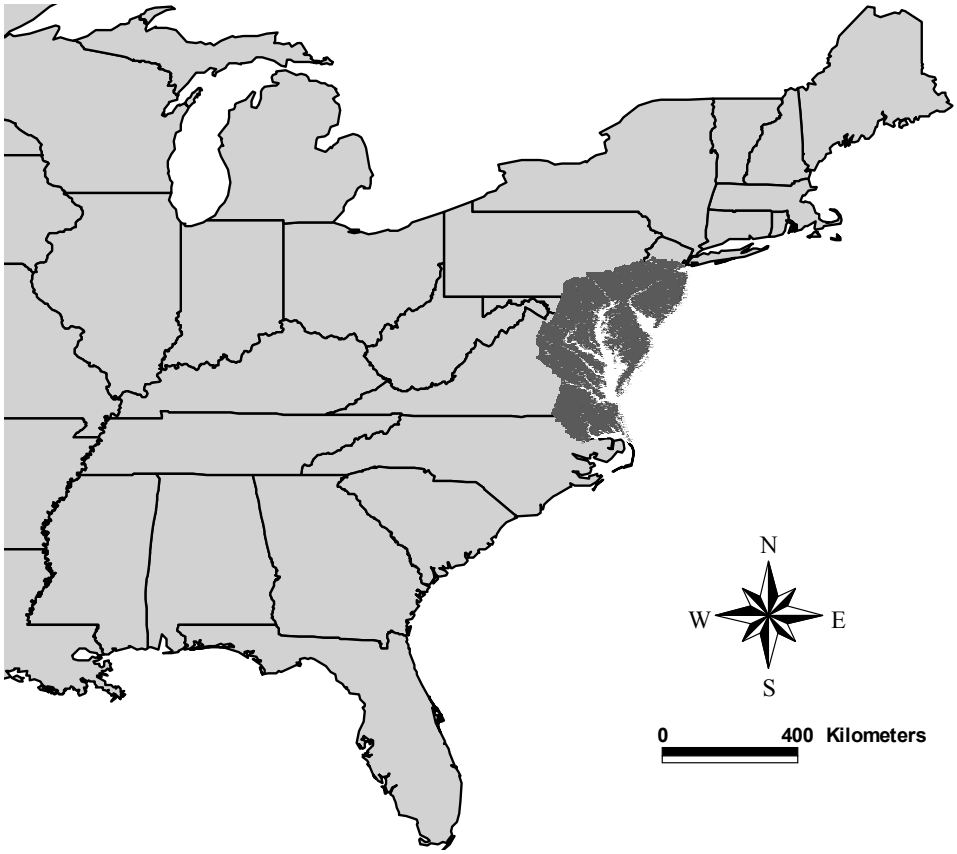

Figure 1. Eastern half of the United States. USGS National Land Cover Data Region 60 is shown in darker gray.

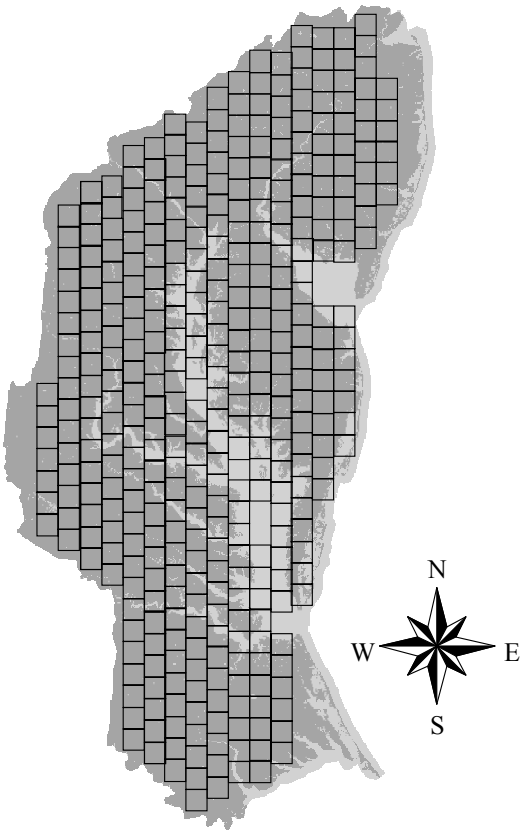

Figure 2. Extent of National Land Cover Data Region 60, encompassing the Chesapeake Bay. Each rectangle represents one sample landscape.

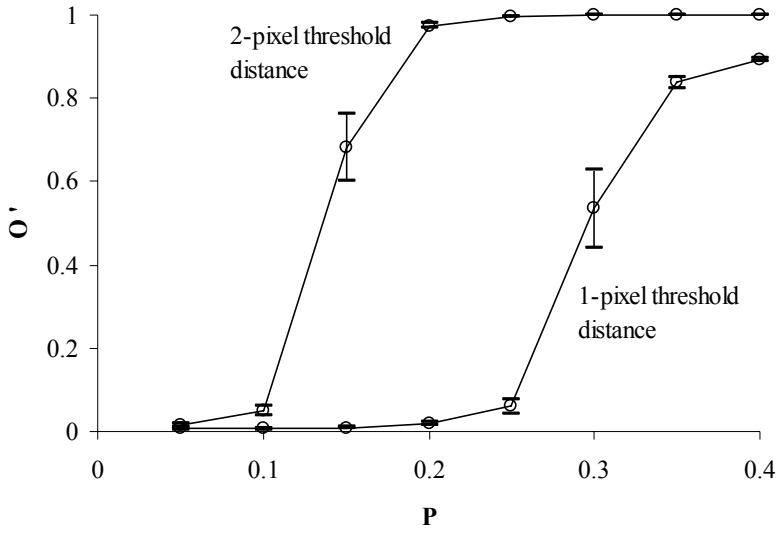

Figure 3. Proportion of habitat patches found in the largest ordered component (O') versus proportion of habitat (P), for 1 and 2-pixel threshold distances on random neutral maps. Circles represent average values from 10 replicate landscapes at each P value (0.05 to 0.4 in increments of P = 0.05), connected by dark solid lines. Vertical lines represent 95% confidence intervals.

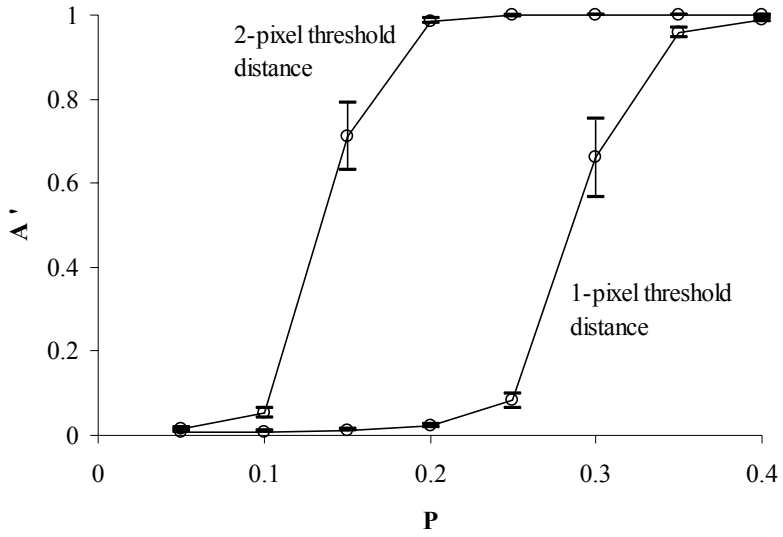

Figure 4. Proportion of habitat area found in the largest ordered component (A') versus proportion of habitat (P), for 1 and 2-pixel threshold distances on random neutral maps. Circles represent average values from 10 replicate landscapes at each P value (0.05 to 0.4 in increments of P = 0.05), connected by dark solid lines. Vertical lines represent 95% confidence intervals.

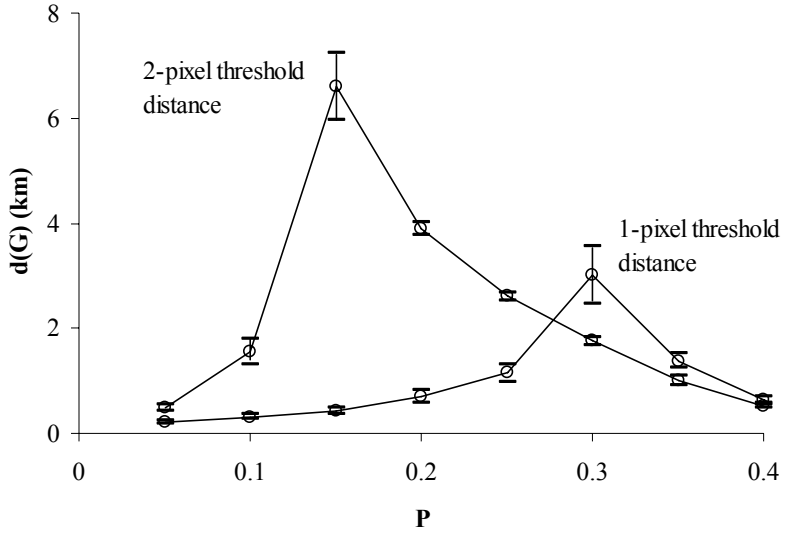

Figure 5. Graph diameter (d(G)) of the largest ordered component versus proportion of habitat (P), for 1 and 2-pixel threshold distances on random neutral maps. Circles represent average values from 10 replicate landscapes at each P value (0.05 to 0.4 in increments of P = 0.05), connected by dark solid lines. Vertical lines represent 95% confidence intervals.

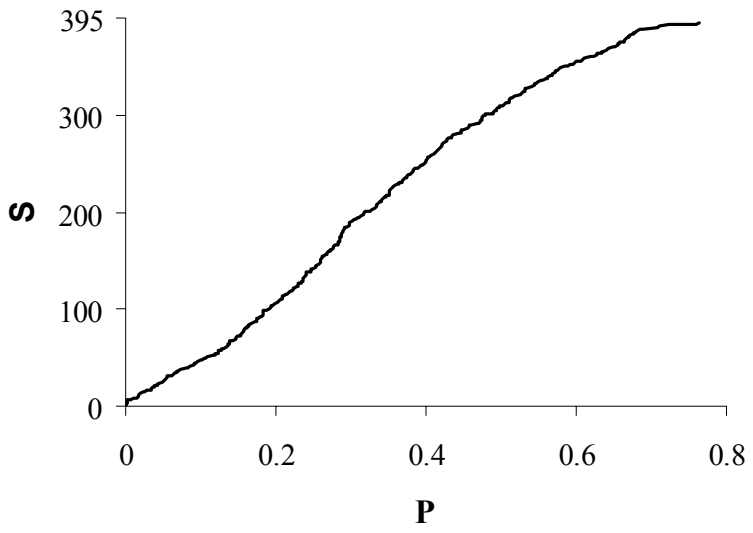

Figure 6. Cumulative frequency distribution of the proportion of forest habitat (P). Sample landscapes were sorted and ranked in ascending order of P, labeled from S = 1 to S = 395 (vertical axis). Horizontal axis shows the proportion of forest habitat (P).

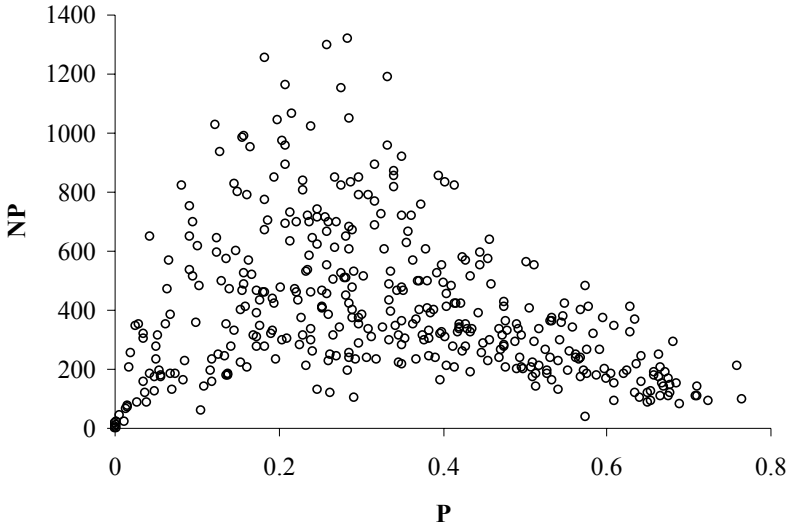

Figure 7. Number of forest patches (NP) versus proportion of forest habitat (P) for 395 sample landscapes.

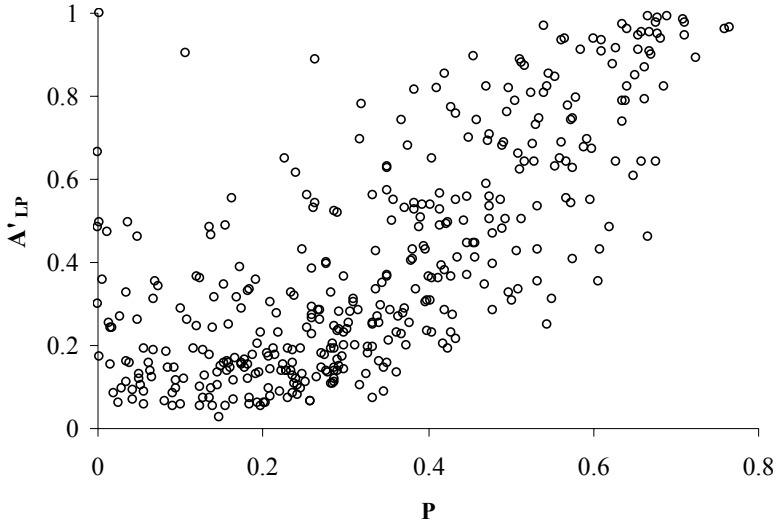

Figure 8. Proportion of forest habitat found in the largest contiguous forest patch (A'_{LP}) versus proportion of forest habitat (P) for 395 sample landscapes.

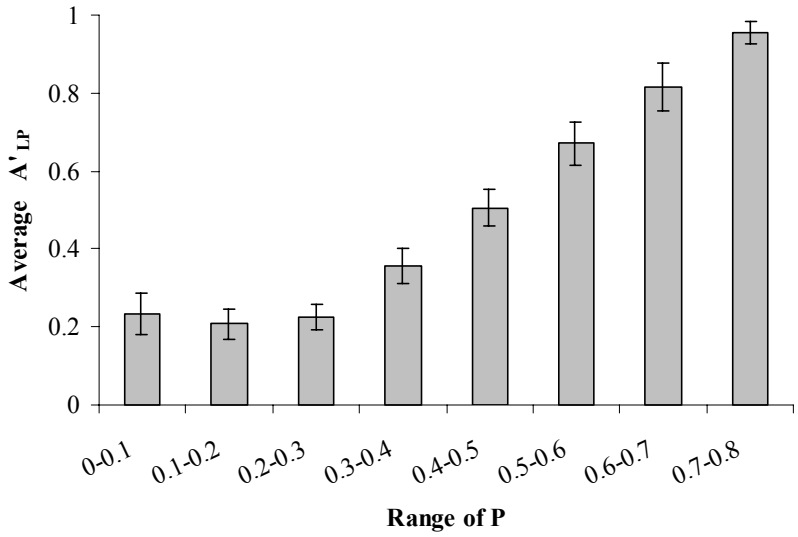

Figure 9. Average value of the proportion of forest habitat found in the largest contiguous forest patch (A'_{LP}) versus proportion of forest habitat (P) from P = 0.0 to P = 0.8 in eight groups of P ranges. Vertical lines represent 95% confidence intervals.

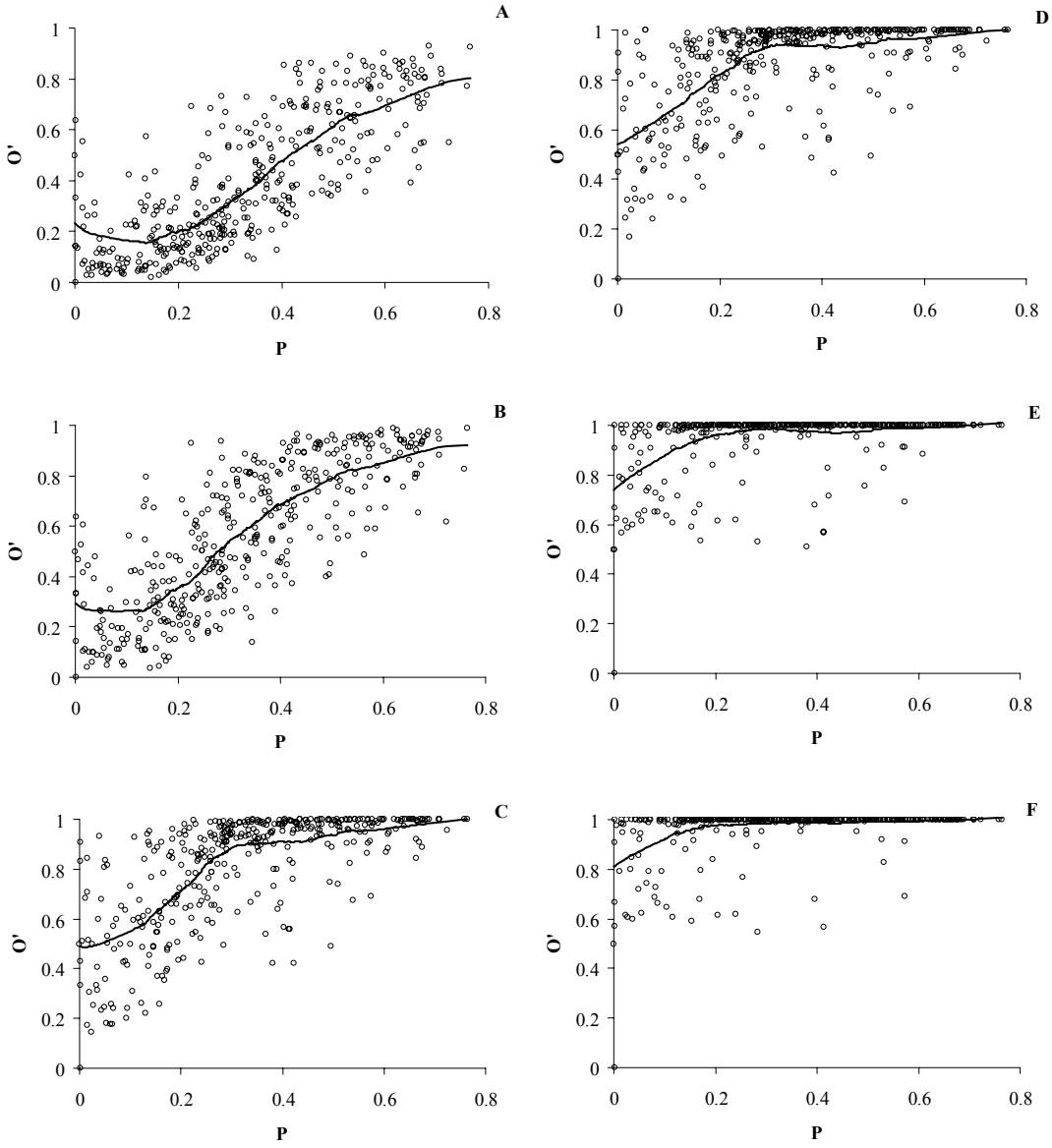

Figure 10. Proportion of habitat patches in the largest ordered component (O'), versus proportion of forest habitat (P), calculated for 395 sample forested landscapes and for threshold distances of 120m (A), 180m (B), 360m (C), 450m (D), 990m (E) and 1,500m (F). Solid line represents LOWESS regression.

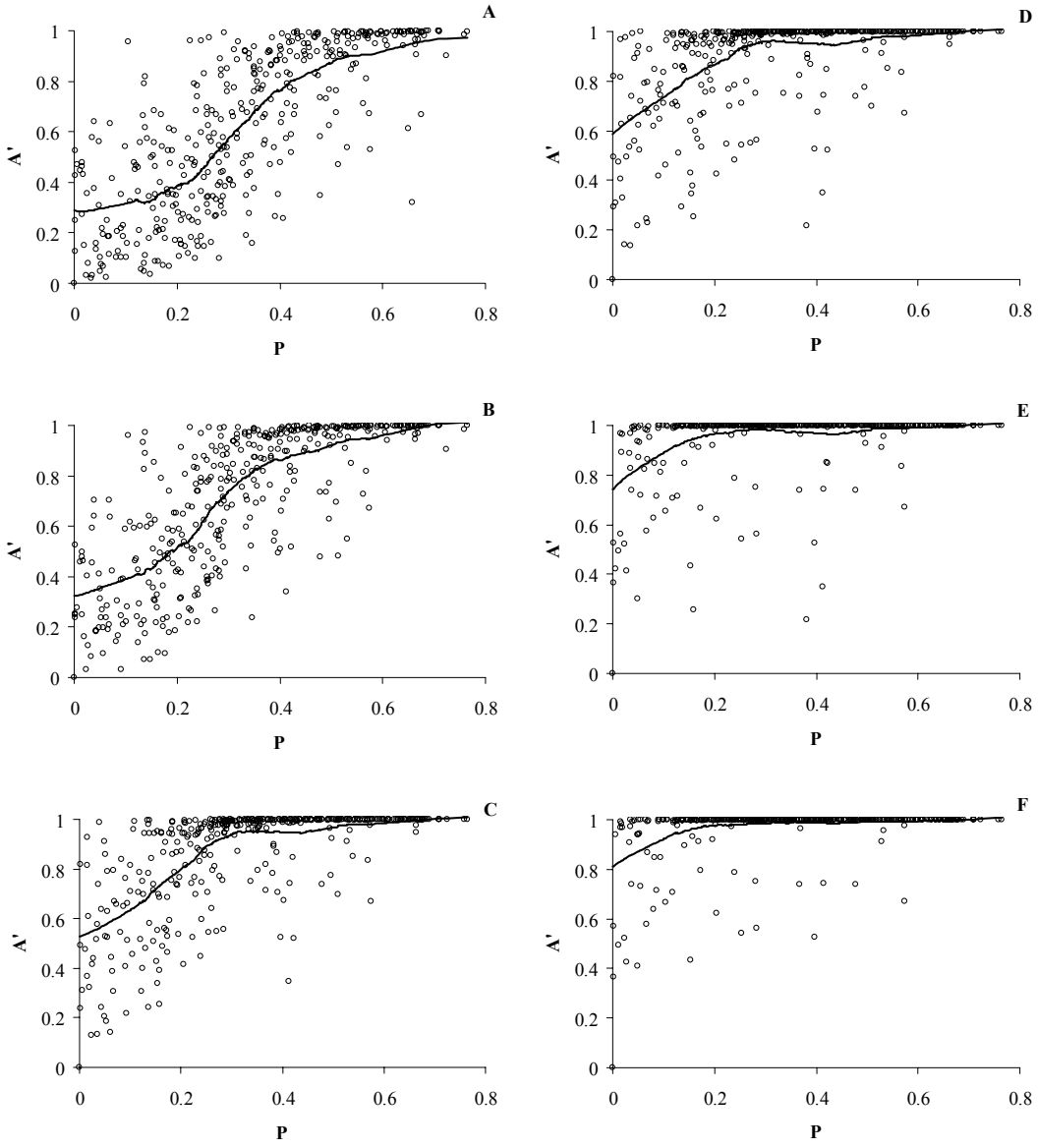

Figure 11. Proportion of habitat area found in the largest ordered component (A') versus proportion of forest habitat (P), calculated for 395 sample forested landscapes and for threshold distances of 120m (A), 180m (B), 360m (C), 450m (D), 990m (E) and 1,500m (F). Solid line represents LOWESS regression.

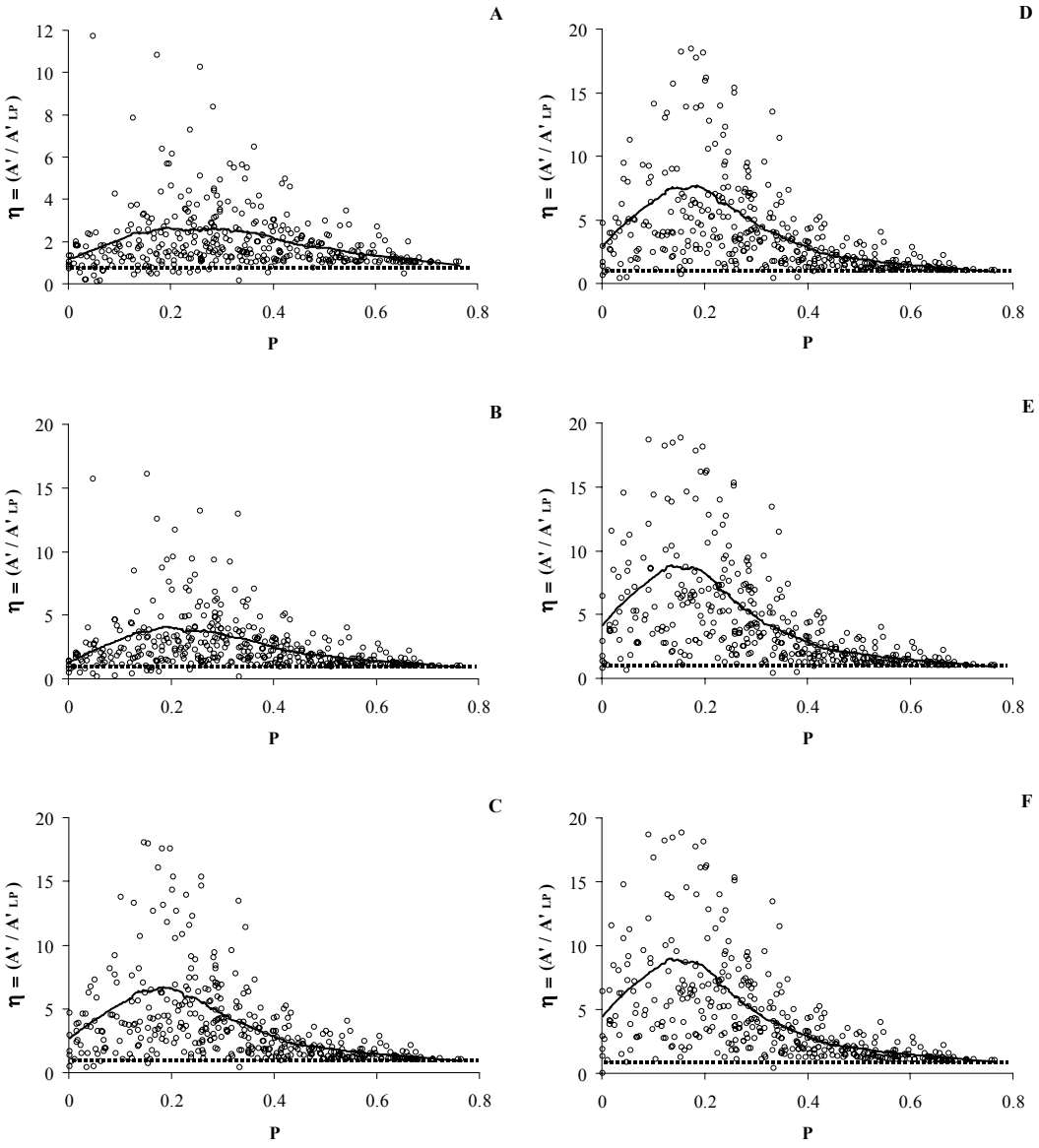

Figure 12. Ratio of the proportion of area in the largest ordered component to that in the largest contiguous patch (η) versus proportion of forest habitat (P), calculated for 395 sample forested landscapes and for threshold distances of 120m (A), 180m (B), 360m (C), 450m (D), 990m (E) and 1,500m (F). Solid line represents LOWESS regression. Data points below dashed horizontal line at η = 1.0 indicate components with a smaller proportion of habitat than is found in the largest contiguous patch.

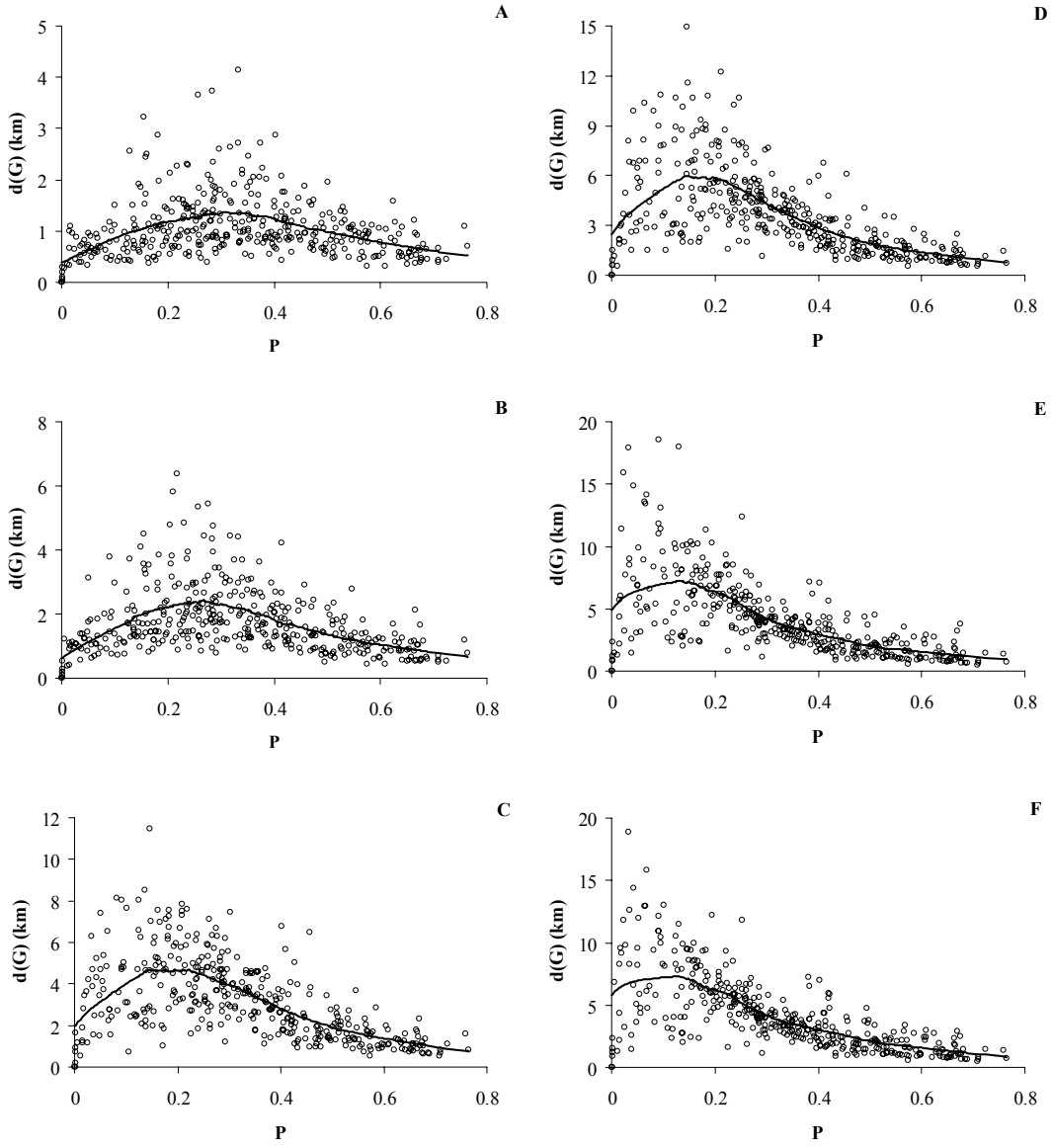

Figure 13. Graph diameter (d(G)) of the largest ordered component versus proportion of habitat forest (P), calculated for 395 sample forested landscapes and for threshold distances of 120m (A), 180m (B), 360m (C), 450m (D), 990m (E) and 1,500m (F). Solid line represents LOWESS regression.

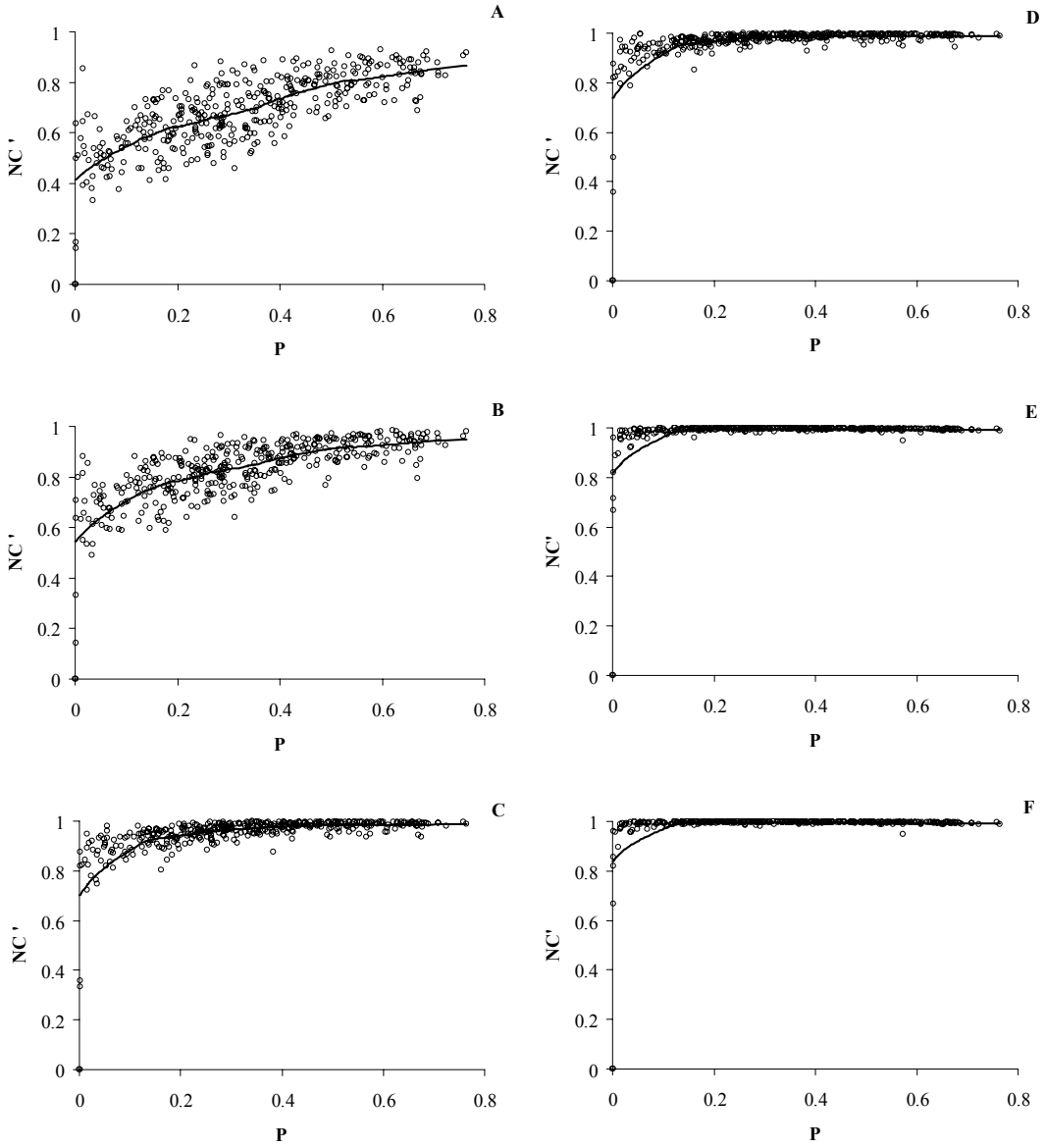

Figure 14. Normalized number of components (NC'), versus proportion of forest habitat (P), calculated for 395 sample forested landscapes and for threshold distances of 120m (A), 180m (B), 360m (C), 450m (D), 990m (E) and 1,500m (F). Solid line represents LOWESS regression.

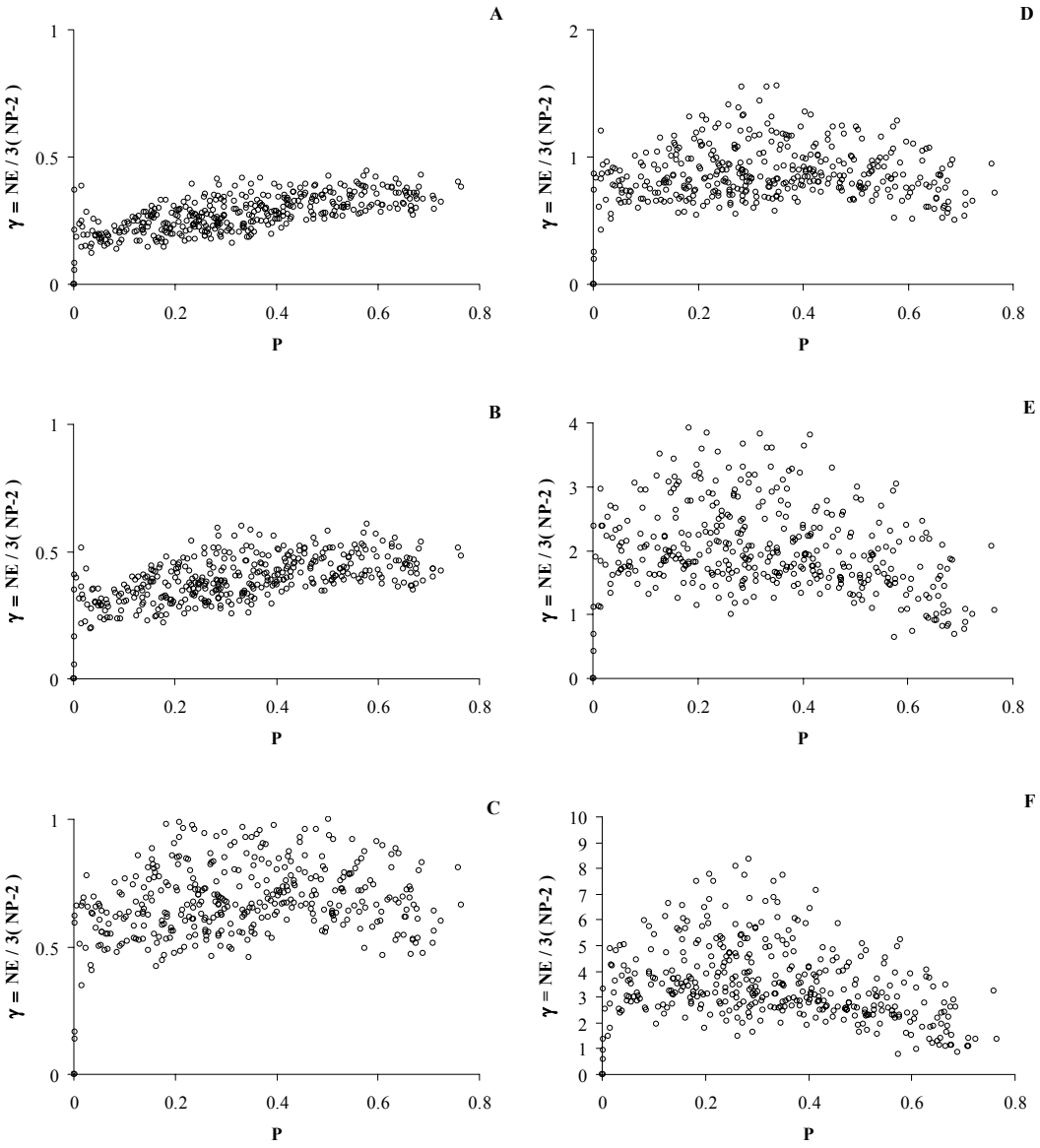

Figure 15. Gamma index (γ), versus proportion of forest habitat (P), calculated for 395 sample forested landscapes and for threshold distances of 120m (A), 180m (B), 360m (C), 450m (D), 990m (E) and 1,500m (F). Note changes in Y-axis values with increasing threshold distance.

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